

A review of the Malvales-feeding psyllid family Carsidaridae (Homoptera)



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Synopsis

The psyllid family Carsidaridae is characterised and considered to be the sister-group of the Homotomidae. It is shown that the monophyletic group, Carsidaridae + Homotomidae, is trophically linked to hostplants of the dicotyledonous superorder Malviflorae. Eight genera, *Epicarsa*, *Carsidara*, *Tyora*, *Tenaphalara*, *Protyora*, *Paracarsidara*, *Mesohomotoma* and a new genus *Allocarsidara*, are recognised in the family; they are diagnosed and a key is given for their identification. It is considered that *Mastigimas* is not a carsidarid and is provisionally placed in the Calophyidae. *Strogylocephala* is confirmed as a good genus, with *Synaphalara* **syn. n.** as its junior synonym; it is removed from the family and placed, again provisionally, in the Calophyidae. Species within each genus are reviewed; six new species are described, eight new combinations are proposed and one subspecies is given species status. Hostplants of all recognised species are restricted to the families Sterculiaceae, Bombacaceae and Malvaceae, within the order Malvales. A phylogeny for the Carsidaridae is proposed which suggests that the group followed the radiation of the Malvales prior to the separation of the African and South American continents.

Introduction

The Psylloidea or jumping plant-lice comprise a group of small, phloem-feeding sternorrhynchous Homoptera with a world-wide distribution. Individual psyllid species show a high degree of hostplant specificity, particularly during the larval stages, and related species tend to develop on related species or groups of dicotyledonous angiosperms. At present about 2000 species are described but collecting in the last 20 years in the tropics and southern temperate regions indicates that the group is probably four times as large.

Until recently the higher classification of the group was based on the Holarctic fauna but this has proved inadequate for the inclusion of the rest of the world's species. With such a

large proportion of undescribed taxa it is useful to be able to classify them into biologically meaningful groups and use their high degree of hostplant specificity to predict probable host ranges.

White & Hodkinson (1985) attempted, with a good measure of success, to produce such a classification based largely on larval morphology and cladistic methodology. It is now desirable to test this classification using adult morphology. White & Hodkinson's Clade 2 (Family Triozidae) has been reviewed (Hollis, 1984) and shown to be a good monophyletic group. They suggested that the sister-group of the Triozidae is the family Carsidaridae (Clade 4) and I attempt here to test the monophyly of this group, discuss its sister-group relationships, diagnose the included genera and review the known species.

Carsidarids are restricted in their hostplant preferences to the families Sterculiaceae, Bombacaceae and Malvaceae within the Malvales, although three recently described Chinese species (Yang & Li, 1985*b*) have been recorded (possibly as vagrants) from other, unrelated families. Each genus that is recognised here is usually restricted to only one of the above families or to the Malvaceae and Bombacaceae together, but the *Mesohomotoma* species-complex seems able to develop on Malvaceae and Sterculiaceae. Several of the host species are of some economic importance, e.g. cocoa (*Theobroma cacao*), durian (*Durio zibethinus*), silk cotton (*Bombax buonopozense* and *B. ceiba*) and kapok (*Ceiba pentandra*); several strong-fibre sources (*Abutilon indicum*, *Firmiana simplex* and *Hibiscus tiliaceus*); and *Heritiera littoralis*, the wood of which is used in boat-building. Psyllid damage to these plants is not well-documented but high infestations of *Tenaphalara acutipennis* on *Bombax ceiba* cause wilting and premature leaf-fall (Sohi & Sandu, 1978), and *Mesohomotoma tessmanni* can cause desiccation and death of terminal shoots of *Theobroma cacao* in Africa (Wood, 1980).

Life history information is available for *Tenaphalara acutipennis* on *Bombax ceiba* (= *malabaricum*) in Bihar, India (Rahman, 1932), *Mesohomotoma tessmanni* on cocoa in Ghana (Kaufmann, 1973) and *Prot'yora sterculiae* on *Brachychiton populneum* in Australia (Froggatt, 1923; Morgan, 1984). In these species the larvae are free-living, tend to feed in aggregations and produce copious amounts of wax during their later stages. Larvae are known for a further nine species and all are morphologically similar, suggesting similar lifestyles.

Little is known of the natural enemies of the group. Cotterell (1927) recorded larvae of the syrphid flies *Baccha sinuata*, *B. praeusta* and *B. picta* feeding on colonies of larvae of *Mesohomotoma tessmanni* in West Africa, and Leston & Gibbs (1968) recorded the mirid bug *Deraeocoris crigi* preying on the same psyllid. Bhatia & Shaffi (1933) recorded the larvae of the syrphid flies *Baccha pulchraformis* and *Sphaerophoria javana* feeding on larvae of *Tenaphalara acutipennis* on *Bombax ceiba* in India.

Materials, methods and terminology

Most of the material studied is deposited in the British Museum (Natural History) (BMNH), with supplementary specimens from the Bernice P. Bishop Museum, Honolulu (BPBM), and the National Museum of Natural History, Washington (USNM). Type material is deposited in BMNH; BPBM; USNM; Australian National Insect Collection, Canberra (ANIC); Beijing Agricultural University Insect Collection, China (BAUIC); Forest Research Institute, Dehra Dun, India (FRI); Institut Royal des Sciences Naturelles de Belgique, Bruxelles (IRSNB); Museum für Naturkunde der Humboldt-Universität, Berlin (MNHU); National Collection of Insects, Plant Protection Research Institute, Pretoria (NCI); Naturhistorisches Museum, Vienna (NM); Osaka Museum of Natural History, Japan (OMNH); and Természettudományi Múzeum, Budapest (TM).

All measurements are quoted in millimetres and were taken from slide-mounted specimens. Reference points, from which measurements were taken of the various structures, are given in Hollis (1976; 1984).

Apart from the head illustrations, all figures were drawn from slide-mounted specimens; setosity of heads and forewings is not shown. The inner surface of the right paramere is shown, apart from Figs 47, 49, 52, 55, which were drawn in anterior view. Dorsal and ventral views of the

caudal areas of larvae are illustrated. Structural terminology follows that of Vondráček (1957) and Hollis (1976; 1984).

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CARSIDARIDAE Crawford

Prionocnemidae Scott, 1882: 466. [Invalid name.]

Prionocnemina Scott; Löw, 1886: 160.

Prionocneminae Scott; Froggatt, 1901: 286; Kieffer, 1906: 387.

Carsidarinae Crawford, 1911: 481, in part; 1914: 53, in part; 1919: 155, in part; Wu, 1935: 126; Tuthill, 1950: 52, in part; Brues *et al.*, 1954: 156; Heslop-Harrison, 1958: 578, in part; Braza & Calilung, 1981: 352, in part; Yang, 1984: 168, in part; Brown, 1985: 245.

Tenaphalarini Heslop-Harrison, 1958: 578, in part.

Carsidaridae Crawford; Klimaszewski, 1964: 12, fig. 7, in part; Bekker-Migdisova, 1973: 98, in part; Morgan, 1984: 118, in part; Brown, 1985: 244, in part.

DIAGNOSIS. Antennal sockets enlarged and swollen ventromedially and vertex often deeply divided by median suture giving the head a 'cleft' appearance in dorsal view; antennal flagellum with a single subapical rhinarium present on flagellomere 3 in addition to those on flagellomeres 2, 4, 6 and 7. False (non-tracheate) *rs-m* crossvein present in forewing or *Rs* and M_{1+2} in broad contact; costal break absent (present in *Protyora*); radular spinules sharply defined into narrow triangular patches, often absent from cu_1 , a patch of spinules present in cell *c+sc*. Ventral sense organs of hind femur in a basal position and not arranged linearly; hind tibia with a well-developed basal spine; hind basitarsus with a single apical spur. Male subgenital plate with a pair of secondary lobes anterior to parameres, these lobes appearing to be sclerotised projections arising from the membrane lining the inner surface of the subgenital plate.

Final instar larva elongate, clearly divided into head, thorax and abdomen; antennae elongate, 10-segmented; legs elongate, tarsal arolium sessile and fan-shaped or globular; wing buds small, without humeral lobes; thoracic sclerites poorly differentiated; caudal region of abdomen differentiated and bearing convoluted pore bands, anus terminal or terminodorsal; body setae mainly simple but scattered, small, lanceolate setae present on caudal sclerites marginally and submarginally.

HOSTPLANTS. Malvales (Sterculiaceae, Bombacaceae and Malvaceae).

DISCUSSION. An historical account of the early conceptual development of the family is given by Hollis (1976: 4). Heslop-Harrison (1958) considered the group as a tribe within the Ciriacreminae including the genera *Carsidara*, *Mastigimas*, *Mesohomotoma*, *Protyora*, *Epicarsa* and *Diceraopsylla*, and separated these genera from another of his Ciriacreminae tribes, the Tenaphalarini, containing *Tenaphalara*, *Stroglycephala*, *Togepsylla* and *Tyora*. Hollis (1984) referred *Diceraopsylla* to the Aphalaridae and White & Hodkinson (1985) placed *Togepsylla* in the same family.

Vondráček (1957: fig. 52) considered the Carsidaridae as the sister-group of the Triozidae, differentiating both families from the Ciriacreminae which he placed in the Psyllidae. Klimaszewski (1964: fig. 7) agreed with these concepts. Bekker-Migdisova (1973) recognised seven subfamilies in her interpretation of the Carsidaridae which amounted to a very large assemblage of many quite unrelated genera.

White & Hodkinson (1985: 242, 273) considerably restricted their concept of the family to the genera *Mastigimas*, *Tenaphalara*, *Protyora*, *Mesohomotoma*, *Paracarsidara*, *Carsidara* and tentatively *Aconopsylla*, *Carsidaroida*, *Nesiopie* and *Tyora*. They placed *Epicarsa* in the Phacopterionidae, considering the anastomosis of *Rs* and M_{1+2} as the important synapomorphy. For reasons given below (p. 90) *Mastigimas* is now removed from the family and placed provisionally in the Calophyidae; *Carsidaroida* and *Nesiopie* are synonyms of *Tyora*, and *Aconopsylla* is referred to the Aphalaridae, close to *Haplaphalara* and *Diclidoph-*

lebia which are also Malvales-feeding. Brown (1985) removed *Epicarsa* from the Phacopterionidae to the Carsidaridae, using the presence of supplementary lobes on the male subgenital plate as a more reliable synapomorphy. This character, and the presence of a non-tracheate *rs-m* crossvein in the forewing, are the best pair of autapomorphies for the Carsidaridae. A crossvein of this type is unique to the family. The supplementary male subgenital lobes occur elsewhere in the Psylloidea only in the Oriental *Cedrela*-feeding genus *Trisetipsylla* Yang & Li (1985a) which, in other characters, is a member of the family Psyllidae. The male hypovalves and tracheate *rs-m* crossvein of *Ciriacremum* (Psyllidae) are not homologues (Hollis, 1976).

White & Hodkinson diagnosed the family on the following larval characters: anal pore field arranged in convoluted bands; dorsal surface of abdomen lacking distinct sclerites; body margin and dorsal surface without setae or derivable structures. To this character-set can be added that poorly defined lanceolate setae are present marginally and submarginally on the caudal plate. These same authors postulated that the Carsidaridae formed the sister-group of the Triozidae, citing the absence of a costal break and the presence of fewer than six apical spurs on the hind tibia as adult synapomorphies, but they suggested no larval synapomorphies. These two adult characters are probably unreliable as they are subject to homoplasy within the Psylloidea generally.

Brown (1985) considered the family to be the sister-group of the *Ficus*-feeding Homotomidae, citing the 'cleft head', weakly sclerotised A_2 vein and the absence of A_1 in the hindwing and a patch of spinules in $c+sc$ of the forewing as synapomorphies. This is a more acceptable hypothesis, although A_1 is present in the hindwing of many homotomids. Further synapomorphies for the two groups are the development of a pair of strong epiphyses on the metapostnotum, and the position and arrangement of the ventral sense organs of the hind femur. The former structures appear to function as 'tethering posts' for both pairs of wings when these are in the resting position. Similar but probably non-homologous structures occur on the metascutellum in some triozids. The basal position of the ventral sense organs on the hind femur is considered to be primitive (Hollis, 1984: 11) but in homotomids and carsidarids they are not linearly arranged and the proximal sensillum is placed at right-angles to the other two.

White & Hodkinson (1985: 274) provisionally placed *Mastigimas* in the Carsidaridae, presumably on larval characters, and Brown (1985) did not dispute this. However the only carsidarid adult character which *Mastigimas* displays is the enlarged antennal sockets giving the head a cleft appearance. The apical rhinarium is absent from the third flagellomere, there is no *rs-m* crossvein, no metapostnotal epiphyses, the forewing radial areas are diffuse, one of the metafemoral sensoria is medial, the basal spine of the hind tibia is absent, there are two apical spurs on the hind basitarsus and there are no supplementary lobes on the male subgenital plate. Furthermore the larva lacks lanceolate setae marginally and submarginally on the caudal plate, and the host plants of all known species are species of *Cedrela* (Meliaceae). For these reasons *Mastigimas* is excluded from the Carsidaridae but this raises the difficult question of where to place the genus in White & Hodkinson's system. A sister-group relationship cannot be argued for it with either the Carsidaridae or the Carsidaridae + Homotomidae and I provisionally place *Mastigimas* near *Apsylla* which White & Hodkinson tentatively referred to the Calophytidae.

The Carsidaridae, as it is recognised here, contains eight genera: *Epicarsa*, *Carsidara*, *Tyora*, *Tenaphalara*, *Protyora*, *Paracarsidara*, *Mesohomotoma* and a new genus, *Allocarsidara*. These are diagnosed below and a key is given for their identification. Nominal species within each genus are discussed in general terms. Insufficient material and incomplete hostplant data prevent thorough revision to species level at present.

Key to genera

- 1 Forewing widening to a broadly rounded apex, Rs and M_{1+2} in broad contact, cu_1 almost as high as wide and with a value of less than 1.3 (Fig. 18); antennal flagellum thickened, 1st flagellar segment short and broad, not more than four times longer than its greatest width (Fig. 2)

EPICARSA (p. 91)
- Forewing narrowing to a subacute apex, Rs and M_{1+2} not in contact but connected by a false *rs-m* crossvein (Figs 19–39), cu_1 much wider than high and with a value of at least 1.6; antennal flagellum elongate, 1st flagellar segment long and narrow, not less than nine times longer than its greatest width 2
- 2 Pterostigma absent and $M+Cu$ about half as long as Cu stem (Figs 36–39); male proctiger bipartite, with a large, anvil-shaped median posterior lobe in addition to lateral lobes (Fig. 77)

MESOHOMOTOMA (p. 106)
- Pterostigma present (Figs 19–31, 35), if absent (Figs 32–34) then $M+Cu$ almost twice as long as Cu stem; male proctiger unipartite, without median posterior lobe, with or without lateral lobes (Figs 40, 43, 46, 51, 57, 66, 75) 3

- 3 *M+Cu* very short, about one-third as long as *R* stem and less than half as long as *Cu* stem (Fig. 19); female terminalia, in profile, rounded dorsally, ventrolateral margins of proctiger with dense fringes of setae, lateral palps ridged (Fig. 79) **CARSIDARA** (p. 92)
- *M+Cu* longer, about as long as or longer than *R* stem and *Cu* stem (Figs 20–35); female terminalia, in profile conical, proctiger sometimes with a median lobe posterior to anal pore, lateral palps not ridged (Figs 80–89) 4
- 4 False *r₁-rs* crossvein present in addition to *rs-m* crossvein (Figs 20–26) 5
- *r₁-rs* crossvein absent (Figs 27–35) 6
- 5 Radular area present in *cu_{1a}*, claval suture reaching hind margin of forewing very close to apex of *Cu_{1b}* (Figs 20–24) **TYORA** (p. 95)
- Radular area absent from *cu_{1a}*, claval suture reaching hind margin of forewing distant from apex of *Cu_{1b}* (Figs 25, 26) **TENAPHALARA** (p. 97)
- 6 Costal break present (Figs 27, 28); apical segment of aedeagus with strongly expanded apex (Fig. 45); male proctiger without lateral expansions (Fig. 43) **PROTYORA** (p. 94)
- Costal break absent (Figs 29–35); apical segment of aedeagus not or only weakly expanded apically (Figs 59, 62, 65, 68, 71, 74, 76); male proctiger with lateral expansions (Figs 57, 60, 63, 66, 69, 72, 75) 7
- 7 Anteorbital lobes strongly developed into ‘horn-like’ structures, lateral and posterior margins of vertex rounded (Figs 11, 12); apex of ductus ejaculatorius enclosed within apical lobes of aedeagus (Figs 59, 62, 65, 68, 71, 74) **ALLOCARSIDARA** (p. 100)
- Anteorbital lobes very weak; lateral margins of vertex sharply raised, posterior margin angular (Figs 14, 15); apex of ductus ejaculatorius extended beyond apical lobes of aedeagus (Fig. 76) **PARACARSIDARA** (p. 104)

EPICARSA Crawford

Epicarsa Crawford, 1911: 488; 1914: 56; Hodkinson & White, 1981: 496; White & Hodkinson, 1985: 241, 243, 272; Brown, 1985: 258. Type-species: *Epicarsa corniculata* Crawford, by original designation and monotypy.

Epicias Caldwell, 1941: 419. [Misspelling.]

Epicasa Caldwell, 1941: 421. [Misspelling.]

DESCRIPTION (only slide-mounted material available for study). Integument of head and thorax very sparsely short setose. Head (Fig. 2) with disc of vertex convex, discal foveae shallow, frontal margin not clearly defined but deeply incised by median suture, lateral and hind margins rounded, lateral ocelli placed anteriorly on vertex, anterolateral tubercles well-developed; antennal sockets enlarged, flagellum short, 2·12 times longer than head width, 1st flagellar segment short and swollen, less than 4 times longer than its greatest width; genal cones present as a pair of small tubercles on either side of mid ventral suture immediately above clypeus; ultimate rostral segment relatively short, less than 3 times longer than its greatest width.

Forewing (Fig. 18) obovate, rounded apically, 2·3–2·6 times longer than wide; costal break absent, pterostigma short and triangular, *r₁-rs* crossvein absent, *Rs* arched downwards towards and in broad contact with *M₁₊₂*, *M+Cu* stem slightly longer than *Cu* stem and about as long as *M* stem, *cu₁* cell value about 1·0 and without radular spinules, apex of claval suture distant from apex of *Cu_{1b}*; hindwing with grouped costal setae; apical spurs of hind tibia arranged 1+2(or 3)+1.

♂ proctiger unipartite with strongly expanded lateral lobes, each with a secondary inwardly pointing subapical lobe.

♀ proctiger abruptly stepped in apical fifth, apical part with a dense covering of short, spine-like setae, apex upcurved (see Ferris, 1928: figs 3a–c); subgenital plate short, similarly stepped apically.

LARVA. Unknown.

HOSTPLANT GENUS. *Ceiba* (Bombacaceae).

COMMENTS. Although possessing most of the features of the family character-suite, the forewing shape, venation and pattern of *Epicarsa* (Fig. 18) is quite unlike other carsidarids. These forewing characters are similar to many homotomids, the carsidarid sister-group, but the similarity may be convergent. Further characters shared between *Epicarsa* and homotomids are the thickened antennal flagellum (Fig. 2) and the bifid lateral lobes of the male proctiger. For these reasons I consider *Epicarsa* to be the sister-group of the rest of the carsidarids.

Brown (1985: 259, fig. 98H) described the endtube of the ductus ejaculatorius of this genus as being

barbed and, from this, suggested a close relationship to the other South American carsidarid genus *Paracarsidara* (and therefore, by inference, to *Mesohomotoma*). I have not examined this character in the holotype of *E. corniculata* and the only other males known (Ferris, 1928) are whole-mount, permanent, microslide preparations in which the structure is obscured.

Included species

Epicarsa corniculata Crawford

(Figs 2, 18)

Epicarsa corniculata Crawford, 1911: 488; 1914: 56; 1925*b*: 56; Ferris, 1928: 244; Costa Lima, 1942: 103; Tuthill, 1950: 58; Hodkinson & White, 1981: 496; Brown, 1985: 260. Holotype ♂, BRAZIL (USNM) [not examined].

Epicarsa corniculata Caldwell, 1941: 419. [Misspelling.]

Epicrasa corniculata Caldwell, 1941: 421. [Misspelling.]

RECORDED DISTRIBUTION. Brazil (Crawford, 1911), Panama (Brown, 1985), Mexico (Ferris, 1928). All other authors refer to these records.

MATERIAL EXAMINED

2 ♂, 2 ♀, **Panama, Mexico** (slide-mounted material of Ferris (1928) and Brown (1985)).

HOSTPLANT. *Ceiba* sp.

CARSIDARA Walker

Carsidara Walker, 1869: 329; Scott, 1882: 466; Kieffer, 1906: 387, in part; Enderlein, 1910: 138; Aulmann, 1913: 79, in part; Heslop-Harrison, 1960: 241; Hodkinson, 1983: 344; 1986: 303. Type-species: *Carsidara marginalis* Walker, by monotypy.

Dynopsylla Crawford, 1915: 264, in part.

Thysanogyna Crawford, 1919: 157; Wu, 1935: 126. Type-species: *Dynopsylla minor* Crawford, by original designation and monotypy. [Synonymised by Crawford, 1924: 619.]

Eustigmia Enderlein, 1921: 119. Type-species: *Dynopsylla minor* Crawford, by original designation and monotypy. [Junior objective synonym of *Thysanogyna*.]

DESCRIPTION. Integument of head and thorax with dense, moderately long setae. Head (Figs 3, 4) with disc of vertex concave, discal foveae clearly marked as broad longitudinal oblique grooves, frontal margin sharply defined and deeply incised by median suture, lateral and hind margins prominent but obtuse, lateral ocelli placed posteriorly on vertex, anterolateral tubercles well-developed; antennal sockets enlarged, flagellum 2.4–2.8 times longer than head width, 1st flagellomere elongate, more than 9 times longer than its greatest width; genae swollen ventrally on either side of median suture anterior to clypeus, each with a prominent papilla, weak lateroventral tubercles also present; apical rostral segment elongate, more than four times longer than its greatest width.

Forewing (Fig. 19) ovate with subacute apex, 2.4–2.9 times longer than wide; costal break absent, pterostigma present, r_1 - rs crossvein absent, $M+Cu$ stem very short, about one-third as long as R stem and 0.4–0.5 times as long as Cu stem, cu_1 cell value 2.33–3.75, without radular spinules, apex of claval suture adjacent to apex of Cu_{1b} ; hindwing with grouped costal setae; apical spurs of hind tibia arranged 1+3+1.

♂ proctiger (Fig. 40) unipartite, lateral lobes moderately developed; apex of basal segment of aedeagus expanded and strongly sclerotised, apical segment of aedeagus highly modified (Fig. 42), endtube of ductus ejaculatorius heavily sclerotised.

♀ proctiger (Fig. 79) without posterodorsal lobe, apex strongly sclerotised and upcurved, posterolateral margins with fringes of long setae; lateral palps heavily ridged.

LARVA. Unknown.

HOST PLANT GENERA. *Brachychiton* and *Firmiana* (Sterculiaceae).

COMMENTS. *Carsidara* is distinct from the rest of the family and is diagnosed by its broader forewing, the very short $M+Cu$ stem in the forewing, the modified distal segment of the male aedeagus and the structure of the female genital apparatus. I regard the genus as the sister-group of the rest of the family less *Epicarsa*.

Included species

Carsidara marginalis Walker

Carsidara marginalis Walker, 1869: 329; Scott, 1882: 467; Aulmann, 1913: 79; Crawford, 1924: 619; Heslop-Harrison, 1960: 237 *et seq.*; Hodkinson, 1983: 344; 1986: 304. Holotype ♀, 'CELEBES' (BMNH) [examined].

Dynopsylla minor Crawford, 1915: 263. Holotype ♂, PHILIPPINES (?USNM) [not examined]. [Synonymised by Crawford, 1924: 619.]

Thysanogyna minor (Crawford) Crawford, 1919: 158; Miyatake, 1981: 37.

Eustigmia minor (Crawford) Enderlein, 1921: 119.

RECORDED DISTRIBUTION. Philippines, Sulawesi, Tanimbar Is.

MATERIAL EXAMINED

1 ♂, 9 ♀, from **Malaya, Hong Kong** (on *Brachychiton rupestris*), **Sabah, Sulawesi**.

HOSTPLANT. *Brachychiton rupestris*.

COMMENTS. Crawford (1919) records slight differences in colour and forewing vein proportions in the Tanimbar Is specimens. The Malayan and Hong Kong material studied differs from Walker's holotype in that there is no brown pattern on the forewing around the radular spinules or apices of M_{1+2} , M_{3+4} or Cu_{1a} , and M_{1+2} is less strongly arched basally. The significance of these differences is not apparent and further material with accurate hostplant data is required.

Carsidara limbata (Enderlein)

Thysanogyna limbata Enderlein, 1926: 397; Wu, 1935: 126. Syntypes ♂, ♀, CHINA [not examined].

Carsidara limbata (Enderlein) Hodkinson, 1986: 303.

RECORDED DISTRIBUTION. Only known from the type-series, 'China. Tsingtau'.

HOSTPLANT. Unknown.

COMMENTS. Enderlein separated this species from *marginalis* (as *minor*) on its larger size (forewing length 5.25–5.75 mm), the brown pattern on the posterior margin of the forewing and some slight venational differences.

Carsidara shikokuensis (Miyatake) **comb. n., stat. n.**

Thysanogyna minor shikokuensis Miyatake, 1981: 37. Holotype ♂, JAPAN: Kashima Is (OMNH) [not examined].

RECORDED DISTRIBUTION. Only known from the type series.

HOSTPLANTS. *Firmiana simplex*; also found on *Mallotus japonicus*.

COMMENTS. Miyatake's figures (1981: figs 1A–G), especially of the male genitalia, show this taxon to be quite distinct from *marginalis* and it is given full species status. However, there is a strong possibility that it is synonymous with *limbata*.

Carsidara africana **sp. n.**

(Figs 3, 4, 19, 40–42, 79)

Body ochraceous to mid brown, mesopraescutum with a dark brown anteromedial patch and mesonotum dark brown laterally; antennal flagellomeres 1–6 dark brown apically, 7–8 entirely dark brown; forewing hyaline, with brown pattern as in Fig. 19.

Head and dorsum of thorax with moderately long, dense setae. Antennal flagellum 2.7–3.0 times longer than head width, 1st flagellomere more than nine times longer than its median width and with 6–12 rhinaria in apical third, 2nd flagellomere with 10–20 rhinaria in apical half, 3rd flagellomere with 5–7 rhinaria in apical quarter, 4th flagellomere with 2 subapical rhinaria and up to 5 more in apical third, 5th flagellomere with 0 or 1 subapical rhinarium and up to 3 more in apical third, 6th flagellomere with 2 subapical rhinaria, 7th flagellomere with a single subapical rhinarium; ultimate rostral segment more than 6 times longer than wide.

Forewing (Fig. 19) 2.47–2.63 times longer than wide and about 1.6 times longer than hindwing;

pterostigma short, less than half as long as R_1 ; $M+Cu$ stem about 0.33 times as long as R stem and about 0.5 times as long as Cu stem, cu_1 value 2.33–3.39.

♂ genitalia as in Figs 40–42; proctiger about 1.4 times longer than wide; paramere with an outwardly directed, rounded, posteroapical lobe in addition to posteroapical hook.

♀ terminalia as in Fig. 79.

Measurements (3 ♂, 1 ♀). Head width, ♂ 0.95–1.01, ♀ 1.01; length of antennal flagellum, ♂ 2.68–2.82, ♀ 2.81; length of ultimate rostral segment, ♂ 0.43–0.45, ♀ 0.48; length of forewing, ♂ 4.98–5.71, ♀ 5.54; length of hind tibia, ♂ 1.08–1.24, ♀ 1.14.

LARVA AND HOSTPLANT. Unknown.

Holotype ♂, **Angola**: 7 mls W. Gabela, 16–18.iii.1972, at light (*D. Hollis*) (BMNH); dry-mounted.

Paratypes. **Ghana**: 2 ♀, Northern Region, Garu, 250 m, N 10.51–W 0.12, 27.x.1971, Nr 510 soil trap (*Endrody-Younga*). **Nigeria**: 1 ♂, Ile-Ife, 26.ii.1970 (*J. T. Medler*). **Uganda**: 2 ♂, Kampala, 7.iii.1933 (*H. Hargreaves*). (BMNH; TM); slide- and dry-mounted.

COMMENTS. The male and female genitalia of this species are remarkably similar to *marginalis* but the two species differ markedly in antennal structure, that of *marginalis* being simple, with a single subapical rhinarium on flagellomeres 2, 3, 4, 6, and 7.

Carsidara sp.

Carsidara sp. Heslop-Harrison, 1960: 241.

A single damaged female of this genus is in BMNH from Madagascar, Nosy Komba. The antennae are missing and I am unable to identify the specimen.

PROTYORA Kieffer

Protyora Kieffer, 1906: 390; Aulmann, 1913: 29; Tuthill & Taylor, 1955: 250; White & Hodkinson, 1985: 242, 273. Type-species: *Tyora sterculiae* Froggatt, by monotypy.

Neocarsidara Crawford, 1925a: 32; 1927: 31; Tuthill & Taylor, 1955: 250. Type-species: *Tyora sterculiae* Froggatt, by monotypy. [Junior objective synonym.]

DESCRIPTION. Integument of head and thorax almost glabrose. Head (Figs 5, 6) with disc of vertex weakly concave, foveae present as broad longitudinal grooves, hind and lateral margins of vertex rounded, anterior margin not sharply defined but deeply incised by median suture, lateral ocelli placed posteriorly on vertex, anterolateral tubercles absent or present; antennal sockets enlarged, antennal flagellum about 3.7 times longer than head width, 1st flagellomere more than 10 times longer than wide; genal cones present as a pair of small tubercles on either side of mid ventral suture immediately anterior to clypeus, lateroventral tubercles absent; ultimate rostral segment 2.7–3.8 times longer than wide.

Forewing (Figs 27, 28) narrow-elongate, 2.9–3.3 times longer than wide, with a narrowly rounded or subacute apex, costal break present, pterostigma present, r_1 - rs crossvein absent, $M+Cu$ stem almost as long as or longer than R stem and Cu stem, cu_1 cell value greater than 2.0, radular spinules absent or very weakly present in cu_1 , apex of claval suture distant from apex of Cu_{1b} ; hindwing with grouped costal setae; apical spurs of hind tibia arranged 1+2+1.

♂ proctiger (Fig. 43) unipartite, flask-shaped, with poorly developed lateral lobes; apex of aedeagus (Fig. 45) with enlarged apical lobes, endtube of ductus ejaculatorius simple.

♀ proctiger (Fig. 80) short, conical in profile, without posterodorsal lobe.

LARVA. Caudal plate as in Fig. 90.

HOSTPLANT GENUS. *Brachychiton* (Sterculiaceae).

COMMENTS. The two main features of this genus are the presence of a costal break in the forewing and the swollen and modified apex of the aedeagus. The costal break is either primitively retained or secondarily derived and, as I consider its absence as a groundplan feature of the family, I postulate the latter. The form of the aedeagal apex is also regarded as a derived character but not strictly homologous with that of *Carsidara*. Apart from the simple, flask-shaped male proctiger, *Protyora* shares other characters, such as the narrow-elongate forewing and long $M+Cu$ stem vein, with the *Tyora* + *Tenaphalara* group and the *Allocarsidara* + *Paracarsidara* + *Mesohomotoma* group; it is regarded as the sister-group of these genera.

Until now *Protyora* was thought to be a purely Australian genus, unique in this respect within the Carsidaridae. The discovery of another species in Indonesia shows the genus to have a closer relationship with the Oriental fauna and to be less isolated.

Tuthill & Taylor (1955) regarded *Neocarsidara* as a nomen nudum but under Article 12(b)(5) of *The International Code of Zoological Nomenclature* (3rd edn) the name is valid. However, it has the same type-species as *Protyora* and is therefore an objective synonym.

Included species

Protyora sterculiae (Froggatt)

(Figs 27, 90)

Tyora sterculiae Froggatt, 1901: 289; 1923: 84. Syntypes ♂, ♀ and larvae, AUSTRALIA (NSW on *Brachychiton populneum*, QLD on *Brachychiton* sp.) (ANIC) [not examined].

Protyora sterculiae (Froggatt) Kieffer, 1906: 390; Aulmann, 1913: 29; Tuthill & Taylor, 1955: 250; Morgan, 1984: 37, 68.

Neocarsidara sterculiae (Froggatt) Crawford, 1925a: 32; 1927: 31. [Invalid combination, Tuthill & Taylor, 1955: 250.]

HOSTPLANT. *Brachychiton populneum* (Sterculiaceae).

RECORDED DISTRIBUTION. Australia (QLD, NSW, SA).

MATERIAL EXAMINED

Adults and larvae from **Australia** (QLD, ACT).

COMMENTS. Brief accounts of the life-history of this species are given by Froggatt (1923) and Morgan (1984). It differs from the new species described below in that the anterolateral tubercles of the vertex are poorly developed, the 1st flagellomere is relatively shorter (10 times longer than its greatest width), the forewing (Fig. 27) is relatively broader (2.9–3.0 times longer than wide) and has a more rounded apex, the pterostigma is broader, *M+Cu* stem is relatively longer, the male parameres and aedeagal apex are of a different shape and the female proctiger is more obtuse apically (Morgan, 1984).

Protyora wilsoni sp. n.

(Figs 5, 6, 28, 43–45, 80)

DESCRIPTION. Similar to *sterculiae*. Differs in that antennal flagellum is 3.28–3.75 times longer than head width and has alternating ochraceous and dark brown rings, 1st flagellomere longer and narrower, about 15 times longer than its greatest width; anterolateral tubercles of vertex more strongly developed.

Forewing (Fig. 28) 3.14–3.25 times longer than wide and with a more acute apex, pterostigma narrow, *M+Cu* stem almost as long as *R* stem and *Cu* stem, *cu₁* cell value 2.35–3.0.

♂ paramere and aedeagal apex as in Figs 44, 45.

♀ proctiger (Fig. 80) more acute and slightly upcurved apically.

Measurements (2 ♂, 2 ♀). Maximum width of head, ♂ 0.70–0.71, ♀ 0.74–0.77; length of antennal flagellum, ♂ 2.51–2.65, ♀ 2.52–2.64; length of ultimate rostral segment, ♂ 0.20, ♀ 0.21; length of forewing, ♂ 3.67–3.70, ♀ 4.24–4.28; length of hind tibia, ♂ 0.62, ♀ 0.66.

LARVA AND HOSTPLANT. Unknown.

Holotype ♂, **Indonesia**: Sulawesi Utara, Dumoga Bone NP, Hogs Back camp, 21.vi.1985, swept (*M. R. Wilson*) (BMNH); dry-mounted.

Paratypes. 2 ♂, 2 ♀, same data as holotype; 1 ♀, 6.vi.1985; 1 ♂, 1 ♀, 25.x.1985 (*M. Asche*); 1 ♀, 13.xi.–4.xii.1985, malaise trap (BMNH); 2 ♂, x.1985 (*Bosmans & Van Stalle*) (IRSNB). Slide- and dry-mounted.

TYORA Walker

Tyora Walker, 1869: 330; Scott, 1882: 470; Kieffer, 1906: 387, in part; Enderlein, 1910: 138; Crawford, 1911: 483; 1920: 355; 1925a: 32; 1927: 30; Aulmann, 1913: 80, in part; Hodkinson, 1983: 366; Yang & Li, 1985b: 206, 215. Type-species: *Tyora congrua* Walker, by monotypy.

Nesiope Kirkaldy, 1908: 389; Aulmann, 1913: 81; Crawford, 1919: 160; Tuthill, 1964: 356; Hodkinson, 1983: 354; 1986: 319. Type-species: *Nesiope ornata* Kirkaldy, by monotypy. [Synonymised with *Carsidaroida* by Crawford, 1919: 161, and with *Tyora* by Crawford, 1920: 355.]

Carsidaroida Crawford, 1917: 164. Type-species: *Carsidaroida heterocephala* Crawford, by original designation and monotypy. [Synonymised by Crawford, 1920: 355.]

DESCRIPTION. Integument of head and thorax very sparsely short haired. Head (Figs 7, 8) with disc of vertex flat or weakly concave, foveae present as shallow circular depressions or furrows, lateral and hind margins of vertex sharply raised, anterior margin sharply defined but weakly incised by median suture, lateral ocellae placed posteriorly on vertex, anterolateral tubercles weak or well-developed; antennal sockets enlarged, flagellum 2.3–3.0 times longer than head width, first flagellomere more than 12 times longer than its median width; genal cones present as a pair of small tubercles on either side of mid ventral line immediately anterior to clypeus, weak lateroventral tubercles also present; occiput with a small tubercle on each side below eye; ultimate rostral segment long, more than 4 times longer than wide.

Forewing (Figs 20–24) narrow, about 3 times longer than wide, with subacute apex, costal break absent, pterostigma present, r_1 - rs crossvein present in addition to rs - m crossvein, $M+Cu$ stem as long as R stem and Cu stem, cu_1 cell value 1.6 or greater and with radular spinules, apex of claval suture adjacent to apex of Cu_{1b} ; hindwing usually with ungrouped costal setae (grouped in *T. striata*); apical spurs of hind tibia arranged 1+2+2.

♂ Proctiger (Figs 46, 48) unipartite, with well-developed lateral lobes; apex of aedeagus narrow, endtube of ductus ejaculatorius slightly swollen (Fig. 50).

♀ proctiger (Figs 81, 82) triangular in profile, usually without posterodorsal lobe (present in *T. striata*).

LARVA. Undescribed (see Miyatake (1965)).

HOSTPLANT GENERA. *Sterculia* and *Heritiera* (Sterculiaceae).

COMMENTS. Like *Tenaphalara* an additional; r_1 - rs crossvein is present in *Tyora* and the apical spurs of the hind tibia are arranged 1+2+2. I regard these two characters as autapomorphies for the two genera. *Tyora* differs from *Tenaphalara* in the raised margins of the vertex, swollen antennal sockets, presence of radular spinules in cell cu_1 , close proximity of the apex of the claval suture to the apex of Cu_{1b} , ungrouped costal setae of the hindwing, well-developed lateral lobes of the male proctiger and the absence of a specialised posterodorsal lobe on the female proctiger, although a simple conical lobe is present in *T. striata*. The two genera are taken to be the sister-group of the *Allocarsidara* + *Paracarsidara* + *Mesohomotoma* complex.

Included species

Further collecting with accurate hostplant data is required before the validity of all the taxa presently included in the genus can be adequately assessed. *T. ornata* and *T. striata* appear to be good species but it is possible that the remainder represents a single species with highly variable forewing pattern.

Tyora buxtoni Crawford

(Figs 22, 46, 47)

Tyora buxtoni Crawford, 1927: 30; 1928: 34; Hodkinson, 1983: 366; Yang & Li, 1985b: 207, 215. Syntypes, 2 ♂, SAMOA [1 ♂ labelled 'Type' in BMNH examined].

HOSTPLANT. Unknown.

RECORDED DISTRIBUTION. Samoa.

MATERIAL EXAMINED

Further specimens with a similar forewing pattern have been examined from various islands in the Solomons group.

COMMENTS. Although the forewing pattern (Fig. 22) is consistently different from *T. congrua*, the male and female genitalia of *buxtoni* are morphologically identical to that species.

Tyora congrua Walker

(Figs 7, 8, 20, 21, 50, 81)

Tyora congrua Walker, 1869: 330; Scott, 1882: 471; Aulmann, 1913: 80; Crawford, 1920: 355; Hodkinson, 1983: 366; Yang & Li, 1985b: 206, 215. Holotype ♂, MYSOL Is [not 'India: Mysore' as in Yang & Li (1985b)] (BMNH) [examined].

Carsidaroida heterocephala Crawford, 1917: 165; 1920: 355. Syntypes ♂, ♀, PHILIPPINES (USNM) [examined]. [Synonymised by Crawford, 1920: 355.]

Nesiopie heterocephala var. *intermedia* Crawford, 1919: 161. Syntypes ♂, ♀ TANIMBAR IS, JAVA [not examined].

HOSTPLANTS. *Sterculia ureolata*, *S. lanceolata* (Sterculiaceae) (BMNH).

RECORDED DISTRIBUTION. Indonesia (Java, Tanimbar Is, Mysol Is), Philippines.

MATERIAL EXAMINED

Adults from **Hong Kong** (on *Sterculia lanceolata*), **West Malaysia** (Pahang), **Indonesia** (Java on *S. ureolata*, Sulawesi Utara, Mysol Is), **Philippines**, **Papua New Guinea** (Morobe Prov., New Britain on *Sterculia* sp.).

COMMENTS. Walker's holotype male is very badly damaged and only part of the thorax, one hind leg, the abdomen and shreds of wing remain. A microslide preparation of the genitalia, made in 1964, has discoloured badly but sufficient remains visible to say that the genitalia are morphologically very similar to those of all other specimens examined. The forewing pattern (Figs 20, 21) varies in extent and intensity in the material studied, being most dense and extensive in specimens from Sulawesi Utara and least so in the Malayan and Hong Kong material.

Tyora guandongana Yang & Li

Tyora guandongana Yang & Li, 1985b: 212, 215. Holotype ♂, CHINA: Guandong (BAUIC) [not examined].

HOSTPLANT. Unknown.

COMMENTS. From the original figures it appears that this species is not distinct from *T. congrua* but, as there is a dark patch of pattern bordering *R+M+Cu* stem and *R* stem (Yang & Li, 1985b: fig. 8b) which is not present in all material of *congrua* examined, formal synonymy is not established.

Tyora ornata (Kirkaldy)

(Figs 23, 48, 49)

Nesiopie ornata Kirkaldy, 1908: 390; Aulmann, 1913: 81; Laing, 1922: 555; Tuthill, 1964: 357; Miyatake: 1965: 175; Hodkinson, 1983: 354. Syntypes (? sex), FIJI [not examined].

Tyora ornata (Kirkaldy) Crawford, 1920: 355; Caldwell, 1942a: 21; Tuthill, 1951: 273; Yang & Li, 1985b: 206, 215.

HOSTPLANT. *Heritiera littoralis* (Sterculiaceae).

RECORDED DISTRIBUTION. Ryukyu Is, N. Borneo, S. Marinana Is, Caroline Is, Fiji.

MATERIAL EXAMINED

Adults from **Fiji** (on *H. littoralis*), **East Malaysia** (Sabah).

COMMENTS. This species is distinguished from *T. congrua* by the shape of the male paramere and the female proctiger and the pattern of the forewing (Figs 23, 49).

Tyora striata (Crawford)

(Figs 24, 82)

Tenaphalara striata Crawford, 1919: 166; Miyatake, 1972: 13; Hodkinson, 1983: 360. Syntypes ♂, ♀, SINGAPORE (USNM) [examined].

Tyora striata (Crawford) Yang & Li, 1985b: 206, 215.

Tenaphalara sulcata Crawford, 1919: 167, nomen nudum [? in error for *striata*].

HOSTPLANT. Unknown.

RECORDED DISTRIBUTION. Singapore.

MATERIAL EXAMINED

Adults from **Singapore** and **Brunei**.

COMMENTS. The presence of a simple posterodorsal lobe on the female proctiger and the grouped costal setae of the hindwing distinguish this species from its congeners.

TENAPHALARA Kuwayama

Tenaphalara Kuwayama, 1908: 155; Aulmann, 1913: 75; Crawford, 1919: 163, in part; Mathur, 1975: 165; Hodkinson, 1983: 360, in part; 1986: 331, in part; Yang, 1984: 181; White & Hodkinson, 1985: 240, 242;

Yang & Li, 1985b: 207, 214. Type-species: *Tenaphalara acutipennis* Kuwayama, by original designation and monotypy.

DESCRIPTION. Integument of head and thorax almost glabrose. Head (Figs 9, 10) with disc of vertex convex, foveae present as very shallow circular depressions, hind and lateral margins of vertex rounded, frontal margin not sharply defined but deeply incised by median suture, lateral ocellae placed posteriorly on vertex, anterolateral tubercles absent; antennal sockets slightly enlarged, antennal flagellum about 2·3 times longer than head width, 1st flagellomere more than 8 times longer than its median width; genal tubercles minute, lateroventral tubercles absent; ultimate rostral segment about 5 times longer than wide.

Forewing (Figs 25, 26) elongate narrow, with subacute apex, about 3·5 times longer than wide, costal break absent, pterostigma present, r_1 - rs crossvein present in addition to rs - m crossvein, $M+Cu$ slightly longer than R stem and slightly longer than Cu stem, cu_1 cell value greater than 2·0 and without radular spinules, apex of claval suture distant from apex of Cu_{1b} ; hindwing with grouped costal setae; apical spurs of hind tibia arranged 1+2+2.

♂ proctiger (Figs 51, 54) unipartite, with or without lateral lobes; apex of aedeagus narrow, endtube of ductus ejaculatorius simple (Figs 53, 56).

♀ proctiger (Fig. 83) with a well-developed dorsal lobe posterior to anal pore.

LARVA. For descriptions of the larval stages of *T. acutipennis* see Rahman (1932) and Yang (1984). The 5th instar larva of *T. pseudonervosa* is described by Mathur (1973). Wax pore ring arrangement of *T. camerunus* as in Fig. 91.

HOSTPLANT GENERA. *Bombax*, *Ceiba* (Bombacaceae).

COMMENTS. *Tenaphalara* is considered here to be the sister-group of *Tyora* but has many more derived features than the latter. The margins of the vertex are rounded, the antennal sockets are much less swollen, the genae bear minute mid ventral tubercles, radular spines are absent from cell cu_1 of the forewing and the apex of the claval suture is distant from the apex of Cu_{1b} , the costal setae of the hindwing are grouped and the female proctiger bears a well-developed and specialised posterodorsal lobe.

The genus has been the most widely misunderstood of the family. The confusion stemming from Crawford's (1919) misinterpretation when he included species belonging to other carsidarid genera, e.g. *malayensis* (Crawford) (see p. 101), *juliana* (Crawford) (see p. 102) and *striata* (Crawford) (see p. 97) and some non-carsidarid species, e.g. *fascipennis* (Crawford) (see p. 99) and *triozipennis* (Crawford) (see p. 100). Yang & Li (1985b) were aware of this confusion and removed several species from *Tenaphalara* but recombined only *fascipennis* and *striata* with more appropriate genera.

Both included and excluded species are listed below with all the latter recombined.

Included species

Tenaphalara acutipennis Kuwayama

(Figs 25, 51–53)

Tenaphalara acutipennis Kuwayama, 1908: 156; Crawford, 1911: 491; 1919: 164 [possible misidentification]; Aulmann, 1913: 75; Ramakrishna Ayyar, 1924: 623; Boselli, 1930: 188; Kuwayama, 1931: 125; Mathur, 1935: 63; 1975: 166; Beeson, 1941: 595; Heslop-Harrison, 1951: 26; Sohi & Sandhu, 1978: 237; Hodkinson, 1983: 360; 1986: 331; Yang, 1984: 181; Yang & Li, 1985b: 206, 214. Syntypes ♂, ♀, JAPAN, ? TAIWAN [not examined].

Tenaphalara elongata Crawford, 1912: 432; 1919: 164; Rahman, 1932: 367; Yang & Li, 1985b: 206, 214.

Syntypes ♂, ♀, INDIA: on 'Silk cotton' [not examined]. [Synonymised by Crawford, 1919: 164.]

Ctenophalara elongata Bhatia & Shaffi, 1933: 545 *et seq.* [Misspelling.].

HOSTPLANTS. *Bombax ceiba* (Bombacaceae). Crawford's (1919) record on *Sterculia foetida* and BMNH specimens on *Hibiscus esculentus* are regarded as doubtful host records.

RECORDED DISTRIBUTION. India, Taiwan, Japan, Philippines.

MATERIAL EXAMINED

Adults and larvae from **Pakistan** (on *Bombax ceiba*), **India**, **Bangladesh** (on *Bombax ceiba* and *Hibiscus esculentus*).

COMMENTS. Most authors have accepted Crawford's synonymy of *elongata* with *acutipennis* but Yang & Li (1985b), basing their judgement on a combination of Kuwayama's (1908) and Mathur's (1975) figures,

regarded *acutipennis* and *elongata* as separate species. Evidence from the BMNH collections suggests that only one species is involved.

***Tenaphalara camerunus* (Aulmann) comb. n.**

(Figs 9, 10, 26, 54–56, 83)

Carsidara camerunus Aulmann, 1912b: 21; 1913: 79. Holotype ♂, CAMEROON (MNHU).

HOSTPLANTS. *Ceiba pentandra*, *Bombax buonopozense* and *B. sessile* (Bombacaceae).

MATERIAL EXAMINED

Adults and larvae from Senegal, Sierra Leone, Ghana, Nigeria, Cameroon, Zaire and Zanzibar.

COMMENTS. Although the holotype has not been examined there are several samples of this species in BMNH collections; a study of these and the original description has shown that *camerunus* should be placed in *Tenaphalara*. The species is similar to *acutipennis* but differs in that the apical segment of the aedeagus is relatively shorter (Fig. 56), the male proctiger has weakly developed lateral lobes (Fig. 54), the paramere is of a different shape (Fig. 55) and the female subgenital plate is trilobed apically (Fig. 83).

***Tenaphalara gossampini* Yang & Li**

Tenaphalara gossampini Yang & Li, 1985b: 208. Holotype ♂, CHINA: on *Bombax ceiba* [as '*Gossampinus malabarica*'] (BAUIC) [not examined].

COMMENTS. From the original figures (Yang & Li, 1985b) of this and the following three species, it is likely that all four are synonyms of *T. acutipennis* but formal synonymy is not established without reference to type material. No larvae were mentioned in the original data for all these species and it is improbable that *Aphanamixis grandifolia* (Meliaceae), *Mangifera indica* (Anacardiaceae) or *Dimocarpus longana* (Sapindaceae) are true hostplants.

***Tenaphalara aphanmixis* Yang & Li**

Tenaphalara aphanmixis Yang & Li, 1985b: 209. Holotype ♂, CHINA: on *Aphanamixis grandifolia* (BAUIC) [not examined].

***Tenaphalara dimocarpi* Yang & Li**

Tenaphalara dimocarpi Yang & Li, 1985b: 211. Holotype ♀, CHINA: on *Dimocarpus longana* (BAUIC) [not examined].

***Tenaphalara mangiferae* Yang & Li**

Tenaphalara mangifera Yang & Li, 1985b: 210. Holotype ♂, CHINA: on *Mangifera indica* (BAUIC) [not examined].

***Tenaphalara pseudonervosa* (Mathur) comb. n.**

Nesiopse pseudonervosa Mathur, 1973: 71; Hodkinson, 1986: 319. Holotype ♂, INDIA: on *Bombax ceiba* (FRI) [not examined].

Tyora pseudonervosa (Mathur) Yang & Li, 1985b: 207, 215.

HOST PLANT. *Bombax ceiba* (Bombacaceae).

COMMENTS. This new combination is made on the basis of the original description; the type material has not been examined. Mathur's figures show a convex vertex, absence of radular spinules from cell *cu*₇ and the characteristically specialised posterodorsal lobe of the female proctiger.

Excluded species

***Stroylocephala fascipennis* Crawford**

Stroylocephala fascipennis Crawford, 1917: 167; Yang & Li, 1985b: 207, 215. Syntypes ♂, ♀, PHILIPPINES (USNM) [examined, all damaged].

Tenaphalara fascipennis (Crawford) Crawford, 1919: 165; Miyatake, 1971: 68.

COMMENTS. Crawford (1919) placed this Philippines species in *Tenaphalara* and synonymised *Strogylocephala* with *Tenaphalara*. This synonymy was accepted by some subsequent authors (Yu, 1957; Miyayake, 1971) but Yang & Li (1985b) disputed this and regarded *Strogylocephala* as a valid genus. Yu (1957) described *Tenaphalara confluens* from Taiwan, on *Palaquium formosanum* (Sapotaceae), and suggested it was closely related to *fascipennis*. Yang & Li (1985b) placed *confluens* also in *Strogylocephala*. Chung Tu Yang (1984) redescribed *confluens* and placed it in a new genus *Synaphalara*, in the subfamily Carsidarinae.

After examining Crawford's type material of *fascipennis* and recently collected specimens of the same species from Sulawesi Utara, on *Palaquium* sp. I agree with Yang & Li (1985b) that *Strogylocephala* is a distinct genus. It is quite unrelated to the Carsidaridae and I tentatively place it in the Calophyidae. Furthermore I consider *Synaphalara* to be a junior synonym of *Strogylocephala* (**syn. n.**) and it is likely that *confluens* and *fascipennis* are synonyms.

Placing *Strogylocephala* in the Calophyidae conflicts with published data on the larva of the type-species which was clearly described as a trioizid larva by Chung Tu Yang (1984: 186). However, when the Sulawesi specimens of *fascipennis* were collected, larvae, which agree generally with Yang's description, and a single adult trioizid were taken at the same time. This trioizid is an undescribed *Trioza* species belonging to the Sapotaceae/Ebenaceae-feeding *obsoleta*-group (Hollis, 1984). It is therefore possible that the larvae described by Yang belong to this trioizid species and are not associated with the *Strogylocephala* species.

***Strogylocephala confluens* (Yu)**

Tenaphalara confluens Yu, 1956: 46. Holotype ♂, TAIWAN [not examined].

Synaphalara confluens (Yu) Chung Tu Yang, 1984: 185.

Strogylocephala confluens (Yu) Yang & Li, 1985b: 207, 216.

COMMENTS. See under *S. fascipennis*.

***Allocarsidara juliana* (Crawford) comb. n.; see below (p. 102)**

***Allocarsidara malayensis* (Crawford) comb. n.; see below (p. 101)**

***Tenaphalara sulcata* Crawford, 1919: 167, nomen nudum; see above (p. 97)**

***Trioza triozipennis* (Crawford) comb. n.**

Tenaphalara triozipennis Crawford, 1919: 167. Holotype ?sex [abdomen missing], SINGAPORE (USNM) [examined].

? *Tenaphalara triozipennis* Crawford; Yang & Li, 1985b: 207, 216.

COMMENTS. The holotype is clearly a trioizid, probably related to *T. umalii* (Miyatake) (see below), and is provisionally placed in *Trioza*.

***Trioza umalii* (Miyatake) comb. n.**

Tenaphalara umalii Miyatake, 1972: 11. Holotype ♀, PHILIPPINES (OMNH) [not examined].

? *Tenaphalara umalii* Miyatake; Yang & Li, 1985b: 207, 216.

COMMENTS. From Miyatake's description there can be little doubt that this species is a trioizid and is probably related to *triozipennis* (Crawford). The above new combination is therefore proposed.

ALLOCARSIDARA gen. n.

[*Tenaphalara* Crawford, 1919: 163, in part; Hodkinson, 1983: 360, in part; 1986: 331, in part; Braza & Calilung, 1981: 354. Misinterpretations.]

Type-species: *Tenaphalara malayensis* Crawford.

DESCRIPTION. Integument of head and thorax almost glabrous. Head (Figs 11, 12) with disc of vertex flat or convex, foveae weak, lateral and hind margins of vertex rounded, anterior margin not clearly defined and weakly incised by median suture, lateral ocelli placed medially on vertex, anterolateral tubercles well-developed; antennal sockets enlarged, flagellum 3.26–4.60 times longer than head width, first flagellomere more than 10 times longer than wide; genal cones present as a pair of very weakly developed

humps on either side of mid ventral line anterior to clypeus, genae also with an outer pair of lateroventral tubercles, occiput with a small tubercle on each side below eye; ultimate rostral segment more than four times longer than wide.

Forewing (Figs 29–34) narrow elongate, at least 2.8 times longer than wide and with an acute apex, costal break absent, pterostigma present or absent, r_1 - rs crossvein absent, $M+Cu$ stem as long as R stem and more than 1.7 times longer than Cu stem, cu_1 cell value 1.76–2.70 and without radular spinules, apex of claval suture distant from apex of Cu_{1b} ; hindwing with grouped costal setae; apical spurs of hind tibia arranged 1+2+1.

♂ proctiger (Figs 57, 60, 63, 66, 69, 72) unipartite, with well-developed lateral lobes that are sometimes subdivided posteroapically, each inner lateral surface with a patch of differentiated spinules; apical segment of aedeagus straight or flexed, aedeagus narrow apically with endtube of ductus ejaculatorius contained within apical lobes (Figs 59, 62, 65, 68, 71, 74).

♀ proctiger (Figs 84–87) with or without a posterodorsal lobe.

LARVA. As in Fig. 92.

HOSTPLANT GENUS. *Durio* (Bombacaceae).

COMMENTS. The sister-group relationship of *Allocarsidara* needs to be resolved. The genus is placed with *Paracarsidara* and *Mesohomotoma* on the structure of the male proctiger but it differs from these genera in having rounded lateral and posterior margins of the vertex, well-developed anterolateral tubercles on the vertex, a simple endtube of the ductus ejaculatorius that is enclosed within the apical lobes of the aedeagus, and a patch of differentiated spinules on each inner lateral surface of the male proctiger. Some species have lost the pterostigma of the forewing as in *Mesohomotoma*.

Yang & Li (1985b) expressed doubt that *Tenaphalara malayensis* Crawford and *T. juliana* Crawford belonged in *Tenaphalara* and this suggestion is confirmed here. Crawford (1919) misinterpreted the genus *Tenaphalara* (see above, p. 98) and his two species *malayensis* and *juliana* are transferred to *Allocarsidara*. A further four new species are described below.

Relationships among these species are not at all clear. A variety of characters appear in the group, e.g. the absence of a pterostigma, an apically bifid male paramere, a flexed distal aedeagal segment, the male proctiger with subdivided lateral lobes, and the female proctiger with a posterodorsal lobe. However, the distribution of these characters within the genus (Table 1) gives little indication of sister-group relationships. The six species included in *Allocarsidara* may be separated from one another by using the character-matrix in Table 1; three are known to develop on *Durio zibethinus*.

Table 1 *Allocarsidara* spp., character-matrix. Primitive condition given in parenthesis.

Character	pterostigma absent (present)	Posterodorsal	♂ paramere truncate (conical)	apical segment of aedeagus flexed (straight)	lateral lobes of ♂ proctiger divided (entire)
		lobe of ♀ proctiger present (absent)			
Species					
<i>malayensis</i>	(-)	+	+	(-)	(-)
<i>iriana</i>	(-)	?	+	(-)	(-)
<i>incognita</i>	(-)	+	(-)	+	+
<i>bakeri</i>	+	?	(-)	+	(-)
<i>juliana</i>	+	(-)	+	+	(-)
<i>elongata</i>	+	+	(-)	(-)	(-)

Included species

Allocarsidara malayensis (Crawford) comb. n.

(Figs 29, 57–59, 86)

Tenaphalara malayensis Crawford, 1919: 165; 1928: 425; Laing, 1930: 39; Hodkinson, 1983: 360; 1986: 332.

Syntypes, ♂, ♀, MALAYA (Penang) and SINGAPORE (USNM) [examined].

? *Tenaphalara malayensis* Crawford; Yang & Li, 1985b: 207, 216.

HOSTPLANT. *Durio zibethinus* (Bombacaceae).

RECORDED DISTRIBUTION. Malaya, Singapore, Sumatra, Java. Braza & Calilung (1981: 355) record this species from the Philippines but their material represents a different species (see below).

MATERIAL EXAMINED

Adults and larvae from **Thailand, Malaya and Java.**

Allocarsidara juliana (Crawford) **comb. n.**

(Figs 32, 66–68, 84)

Tenaphalara juliana Crawford, 1919: 166; 1920: 355; Hodkinson, 1983: 360. Holotype, ? sex, 'BORNEO' (BPBM) [examined].

? *Tenaphalara juliana* Crawford; Yang & Li, 1985b: 207, 216.

LARVA AND HOSTPLANT. Unknown.

RECORDED DISTRIBUTION. Sabah.

MATERIAL EXAMINED

Holotype (? sex), **East Malaysia:** Sabah ('Sandakan, Borneo, Baker'); 1 ♂, 1 ♀, same data as holotype (USNM); 2 ♀, Sarawak, offshore gas platform (BMNH).

COMMENTS. This species was described from a single specimen of unknown sex (the posterior half of the abdomen was missing) from Sabah, and further recorded (Crawford, 1920) from a single female from an unstated locality but presumably in Borneo as the paper in which the specimen is recorded deals with Bornean psyllids. Apart from the holotype (BPBM), there are three specimens bearing the type data, under the name '*Tenaphalara juliana*', in USNM; two complete males and a complete female. The two males are not conspecific with each other and neither can be positively identified as the same species as the damaged holotype of *juliana*. The complete female agrees well with the holotype and I assume that it is the specimen Crawford recorded as *Tenaphalara juliana* in 1920. As well as the locality label this specimen also bears a handwritten label '11734', which is almost certainly an original Baker collection label. One of the two males also bears a similar label and, therefore, I regard it as having been collected by Baker at the same time as the female. I consider this specimen to be the male of *Allocarsidara juliana* and figure it below (Figs 32, 66–68). The other male in USNM is described below as *A. bakeri* sp. n. (p. 103).

Allocarsidara juliana differs from *malayensis* in lacking a pterostigma in the forewing (Fig. 32), lacking a posterodorsal lobe on the female proctiger (Fig. 84) and having a flexed apical aedeagal segment in the male (Fig. 68). It is apparently closest to *bakeri* (see below) but differs from that species in the shape of the paramere (Figs 67, 70).

Allocarsidara incognita sp. n.

(Figs 30, 72–74, 85, 92)

[*Tenaphalara malayensis* Crawford; Braza & Calilung, 1981: 355. Misidentification.]

DESCRIPTION (only slide-mounted and spirit-stored material available for study). Antennal flagellum 3.83–4.30 times longer than head width, 1st flagellomere more than 13 times longer than wide; ultimate rostral segment 1.52–2.17 times longer than flagellomeres 7+8 together.

Forewing (Fig. 30) 2.99–3.18 times longer than wide, pterostigma present, *Cu* stem 3 times longer than *Cu_{1b}*, *cu₁* cell value 1.83–2.62.

♂ genitalia as in Figs 72–74; lateral lobes of proctiger each with a supplementary apicoposterior lobe; paramere narrow apically and with an inwardly directed spine, apical segment of aedeagus flexed.

♀ terminalia as in Fig. 85, proctiger with a well-developed posterodorsal lobe.

Measurements (7 ♂, 7 ♀). Maximum width of head, ♂ 0.67–0.71, ♀ 0.71–0.74; length of antennal flagellum, ♂ 2.67–2.90, ♀ 2.74–3.06; length of ultimate rostral segment. ♂ 0.26–0.30, ♀ 0.30–0.31; length of forewing, ♂ 3.32–3.53, ♀ 3.65–3.89; length of hind tibia, ♂ 0.68–0.76, ♀ 0.71–0.74.

LARVA. Abdominal wax pore rings as in Fig. 92.

HOSTPLANT. Adults and larvae collected from *Durio zibethinus* (Bombacaceae).

Holotype ♂, **Indonesia**: Sulawesi Utara, Dumoga Bone NP, Bungalows light trap, 21.xi.1985 (*RESL Project Wallace*) (BMNH); slide-mounted.

Paratypes. **Indonesia**: 1 ♀, same locality data as holotype, Base Camp light trap, 26.x.1985. **Philippines**: 1 ♀, Davao Exp. Stn, ground level trap, xi.1962 (*M. R. Gavarra*); 2 ♂, 2 ♀, larvae, Davao City, 2.x.1975, *Durio zibethinus* (*M. Gavarra*). **East Malaysia**: 5 ♂, 4 ♀, Sarawak, vi.1963, Maize (*C. R. Wallace*) (BMNH).

COMMENTS. This species is very similar to *malayensis* but can be recognised by the structure of the male genitalia; females of the two species are very difficult to separate from one another.

Allocarsidara iriana sp. n.

(Figs 11–13, 31, 63–65)

DESCRIPTION. Body mid brown dorsally and laterally, ochraceous ventrally; head black but with a median longitudinal pale stripe on vertex, apices of anterolateral tubercles ochraceous; antenna with scape and pedicel ochraceous, flagellum black; forewing hyaline; femora ochraceous, brown anterodorsally, fore and mid tibiae and tarsi dark brown, hind tibia and tarsus ochraceous.

Antennal flagellum relatively short, 3.26 times longer than head width, first flagellomere 10 times longer than its greatest width, seventh flagellomere with a very long subapical seta (Fig. 13); ultimate rostral segment 1.46 times longer than flagellomeres 7+8 together.

Forewing (Fig. 31) 2.86 times longer than wide, pterostigma present, *M+Cu* stem just over twice as long as *Cu* stem, *Cu* stem twice as long as *Cu_{1b}*, *cu₁* value 2.13.

♂ genitalia as in Figs 63–65; lateral lobes of proctiger short, not subdivided posteroapically; paramere broad apically, with an anteriorly directed spine and an apicoposterior tubercle; apical segment of aedeagus straight.

♀ unknown.

Measurements (1 ♂). Maximum width of head, 0.58; length of antennal flagellum, 1.88; length of ultimate rostral segment, 0.23; length of forewing, 3.00; length of hind tibia, 0.76.

LARVA AND HOSTPLANT. Unknown.

Holotype ♂, **New Guinea**: NW, Nabire, S. Goelvink Bay, 7.ix.1962, light trap in jungle (*H. Holtman*) (BPBM); slide-mounted.

COMMENTS. The forewing of this species has a pterostigma, as in *malayensis* and *incognita*, but it may be recognised by the shape of the male paramere and aedeagus, the relatively short antennal flagellum and the long subapical seta on flagellomere seven.

Allocarsidara bakeri sp. n.

(Figs 33, 69–71)

DESCRIPTION. Body light brown, head darker; antenna with scape, pedicel and first flagellomere dark brown, rest of flagellum lighter; forewing hyaline; legs ochraceous, fore and mid femora with dark anterodorsal stripes, mid tibia and tarsus darker.

Antennal flagellum 4.66 times longer than head width, first flagellomere 12 times longer than its greatest width.

Forewing (Fig. 33) 3.45 times longer than wide, pterostigma absent, *Cu* stem 3.5 times longer than *Cu_{1b}*, *cu₁* cell value 2.7.

♂ genitalia as in Figs 69–71; lateral lobes of proctiger long but not subdivided posteroapically; apex of paramere narrow and with an inwardly directed curved spine; apical segment of aedeagus flexed.

♀ unknown.

Measurements (1 ♂). Maximum width of head, 0.59; length of antennal flagellum, 2.77; length of ultimate rostral segment, 0.24; length of forewing, 3.12; length of hind tibia, 0.57.

LARVA AND HOSTPLANT. Unknown.

Holotype ♂, **East Malaysia**: Sabah; 'Sandakan, Borneo, Baker' (USNM); slide-mounted.

COMMENTS. This species is very similar to *juliana* but differs in that the lateral lobes of the male proctiger are longer (Figs 66, 69), the paramere is narrow apically (Figs 67, 70), the apex of the aedeagus is of a different shape (Figs 68, 71) and the forewing is relatively narrower (3.10 times longer than wide in *juliana*).

Allocarsidara elongata sp. n.

(Figs 34, 60–62, 87)

DESCRIPTION (only slide-mounted and spirit-preserved material available for study). Antennal flagellum 3.98–4.60 times longer than head width, first flagellomere 16 times longer than its greatest width; ultimate rostral segment relatively long, 2.54–2.89 times longer than flagellomeres 7+8 together.

Forewing (Fig. 34) 3.21–3.35 times longer than wide, pterostigma absent, *Cu* stem about 4 times longer than *Cu*_{1b}, *cu*₁ cell very small.

♂ genitalia as in Figs 60–62; lateral lobes of proctiger undivided posteroapically; apex of paramere narrow, with a large and inwardly directed apical tubercle; apical segment of aedeagus straight.

♀ terminalia as in Fig. 87, proctiger with a well-developed posterodorsal lobe.

Measurements (6 ♂, 7 ♀). Maximum width of head, ♂ 0.64–0.73, ♀ 0.69–0.75; length of antennal flagellum, ♂ 2.83–3.00, ♀ 3.11–3.26; length of ultimate rostral segment, ♂ and ♀ 0.31–0.33; length of forewing, ♂ 3.47–3.59, ♀ 3.81–4.14; length of hind tibia, ♂ 0.69–0.73, ♀ 0.71–0.74.

HOSTPLANT. Adults and larvae collected from *Durio zibethinus* (Bombacaceae).

Holotype ♂, West Malaysia: Malaya, Alor Star, Jitra, 3.xii.1985, *Durio zibethinus* (N. K. Ho) (BMNH); slide-mounted.

Paratypes. 7 ♂, 9 ♀, same data and depository as holotype; slide- and dry-mounted.

COMMENTS. This species resembles *juliana* and *bakeri* in lacking a pterostigma in the forewing; it differs from both in having a straight apical aedeagal segment, and from *juliana* in having an apically narrow paramere and a well-developed posterodorsal lobe on the female proctiger.

PARACARSIDARA Heslop-Harrison

[*Carsidara* Walker; Crawford, 1911: 484; 1914: 57; Tuthill & Taylor, 1950: 53; Brues *et al.*, 1954: 156; Morgan, 1984: 19, fig. 15. Misinterpretations.]

Paracarsidara Heslop-Harrison, 1960: 244; Hodkinson & White, 1981: 505; Brown, 1985: 246. Type-species: *Carsidara dugesii* Löw, by original designation.

DESCRIPTION. Integument of head and thorax almost glabrous. Head (Figs 14, 15) with disc of vertex concave, foveae present as deep oblique grooves, lateral margins of vertex sharply raised, posterior margin angular, anterior margin sharply defined and deeply incised by median suture, lateral ocellae placed posteriorly on vertex, anterolateral tubercles very weak or absent; antennal sockets swollen, flagellum 2.5–3.5 times longer than head width, 1st flagellomere more than 10 times longer than its greatest width; genae with a pair of small mid ventral tubercles anterior to clypeus, each gena with a larger lateroventral tubercle; occiput, on each side below, eye with a small tubercle or swelling; ultimate rostral segment more than 6 times longer than wide.

Forewing (Fig. 35) narrow-elongate, about 2.8 times longer than wide and with a subacute apex, costal break absent, pterostigma present, *r*₁-*rs* crossvein absent, *M*+*Cu* stem almost as long as *R* stem and *Cu* stem, *cu*₁ cell value greater than 2.7 and without radular spinules, apex of claval suture distant from apex of *Cu*_{1b}, costal setae of hindwing grouped; apical spurs of hind tibia arranged 1+3+1.

♂ proctiger (Fig. 75) unipartite, expanded basally and with 2 small apicolateral lobes; aedeagus narrow apically, sometimes lobed basoventrally, endtube of ductus ejaculatorius enlarged and with lateral and apical hooks (Fig. 76).

♀ terminalia (Fig. 88) conical, proctiger more or less 'stepped' posteriorly, apical part narrow and bearing short, thick, spiniform setae and sometimes an apical hook.

LARVA. Caudal plate as in Fig. 93.

HOSTPLANT GENERA. *Ceiba* (Bombacaceae), *Malva* and *Wissadula* (Malvaceae).

COMMENTS. On the basis of the narrow-elongate forewing, absence of *r*₁-*rs* crossvein, long *M*+*Cu* stem, presence of lateral lobes on the male proctiger and narrow apex of the aedeagus, *Paracarsidara* is grouped with *Allocarsidara* and *Mesohomotoma*. The modified endtube of *Paracarsidara* is very similar to that of *Mesohomotoma* and is used as a synapomorphy for these two genera. Brown (1985) also related *Paracarsidara* to *Mesohomotoma*, even doubting their separate identities, but I regard the absence of a pterostigma and the bipartite male proctiger that bears a median posterior lobe in addition to the lateral lobes sufficient to recognise the latter genus.

Included species***Paracarsidara dugesii* (Löw)**

(Figs 75, 76, 88, 93)

Carsidara dugesii Löw, 1886: 160; Crawford, 1911: 486; 1914: 58; Aulmann, 1913: 79; Laing, 1923: 698; Caldwell, 1941: 421, 1944: 58; Tuthill, 1950: 53; Silva *et al.*, 1968: 200 [?misidentification]. Syntypes ♂, ♀, MEXICO: 'planta Malvacea' (NM) [not examined].

Paracarsidara dugesii (Löw) Heslop-Harrison, 1960: 246; Hodkinson & White, 1981: 506; Brown, 1985: 250.

Carsidara concolor Crawford, 1911: 484; 1914: 58; Caldwell, 1942*b*: 28; Caldwell & Martorell, 1951: 604. Syntypes ♂, ♀, CUBA (USNM). [Synonymised by Heslop-Harrison, 1960: 246.]

Paracarsidara concolor (Crawford) Heslop-Harrison, 1960: 246; Hodkinson & White, 1981: 505. [*Carsidara gigantea* Crawford; Laing, 1923: 698. Misidentification.]

HOSTPLANTS. *Malva* sp., *Wissadula perplicifolia* (Malvaceae). Silva *et al.* (1968) record this species from Brazil, on *Bombax cyathophorum* (Bombacaceae), but this is likely to be a misidentification.

RECORDED DISTRIBUTION. Mexico, Guatemala, Cuba, Puerto Rico, Dominica and Jamaica; [?Brazil].

MATERIAL EXAMINED

Adults and larvae from **Mexico and Jamaica** (on *Wissadula perplicifolia*).

***Paracarsidara gigantea* (Crawford)**

(Figs 14, 15, 35)

Carsidara gigantea Crawford, 1911: 486; 1914: 57; Ferris, 1928: 244; Caldwell, 1941: 421. Syntypes ♀, NICARAGUA (USNM).

Paracarsidara gigantea (Crawford) Heslop-Harrison, 1960: 246; Hodkinson & White, 1981: 506; Brown, 1985: 253.

HOSTPLANTS. *Ceiba* sp., *C. burchellii* (BMNH).

RECORDED DISTRIBUTION. Mexico, Guatemala, Belize, Nicaragua, St Kitts, Cuba, Colombia, Brazil.

MATERIAL EXAMINED

Adults and larvae from **Mexico, Panama and Brazil** (on *Ceiba burchellii*).

COMMENTS. Tuthill (1950) synonymised this species with *dugesii* but Brown (1985) considered it to be distinct after examining relevant type material.

***Paracarsidara rostrata* (Crawford)**

Carsidara rostrata Crawford, 1911: 486; 1914: 58; Tuthill, 1950: 53. Syntypes ♀, NICARAGUA (USNM).

Paracarsidara rostrata (Crawford) Heslop-Harrison, 1960: 246; Hodkinson & White, 1981: 506; Brown, 1985: 256.

HOSTPLANT. Unknown.

RECORDED DISTRIBUTION. Nicaragua, Panama.

COMMENTS. Crawford (1914) regarded this species as a synonym of *dugesii* and this was followed by Tuthill (1950). Heslop-Harrison raised *rostrata* from synonymy and Brown (1985) confirmed this after examining type material.

Nomen dubium

Carsidara mexicana Crawford, 1911: 487; 1914: 58 (as a possible synonym of *dugesii*). Holotype ♂, MEXICO [specimen missing from pin, USNM].

Paracarsidara mexicana (Crawford); Heslop-Harrison, 1960: 246; Hodkinson & White, 1981: 248 (as a nomen dubium).

Undescribed species

Brown (1985) recorded two undescribed species from Panama and there are some poorly preserved specimens of a further undescribed species from Trinidad on *Malachra alceifolia* (Malvaceae) in BMNH.

MESOHOMOTOMA Kuwayama

Mesohomotoma Kuwayama, 1908: 180; Aulmann, 1913: 36; Crawford, 1920: 356; 1925a: 32; Tuthill & Taylor, 1955: 249; Miyatake, 1971: 58; Mathur, 1975: 144; Braza & Calilung, 1981: 356; Hodkinson, 1983: 352; 1986: 317; Yang, 1984: 178; White & Hodkinson, 1985: 242. Type-species: *Mesohomotoma camphorae* Kuwayama, by original designation and monotypy.

Udamostigma Enderlein, 1910: 138. Type-species: *Tyora hibisci* Froggatt, by original designation and monotypy. [Synonymised by Crawford, 1920: 356.]

[*Tyora* Walker; Crawford, 1919: 159. Misinterpretation.]

[*Tyor[i]a* Walker; Uichanco, 1921: 279. Misinterpretation; misspelling.]

DESCRIPTION. Integument of head and thorax almost glabrous. Head (Figs 16, 17) with disc of vertex deeply divided by median suture, foveae present as deep oblique grooves, lateral and hind margins of vertex obliquely raised, anterior margin poorly defined but deeply incised by median suture, anterolateral tubercles well-defined, lateral ocellae posteriorly placed; antennal sockets enlarged, flagellum 2.4–3.0 times longer than head width, 1st flagellomere at least 9 times longer than its median width; genae with a small tubercle on either side of mid ventral suture immediately anterior to clypeus, lateral tubercles absent; occiput with a small tubercle on each side below eye; ultimate rostral segment at least 5 times longer than wide.

Forewing (Figs 36–39) narrow, elongate, 2.5–3.0 times longer than wide, with subacute apex; costal break, pterostigma and r_1 -rs absent, $M+Cu$ stem short, about two-fifths as long as R stem and half as long as Cu stem, cu_1 cell value almost 2.0 and without radular spinules, Cu_{1a} strongly arched towards M stem, apex of claval suture distant from apex of Cu_{1b} ; costal setae of hindwing grouped; apical spurs of hind tibia arranged 1+3+1.

♂ proctiger (Fig. 77) bipartite, a strong anvil-shaped median posterior lobe present in addition to well-developed lateral lobes; aedeagus (Fig. 78) narrow apically, apex of ductus ejaculatorius prominent, strongly produced from aedeagal apex and expanded apically.

♀ proctiger (Fig. 89), in profile, strongly stepped posteriorly, apical part narrow elongate and bearing short and thickened setae, apex weakly barbed.

LARVA. Caudal plate as in Fig. 94. Larval stages of *M. camphorae* described by Yang (1984).

HOSTPLANT GENERA. *Hibiscus*, *Thespesia*, *Abutilon*, *Urena* (Malvaceae); *Cola*, *Theobroma*, *Sterculia*, *Heritiera* (Sterculiaceae).

COMMENTS. *Mesohomotoma* differs from all other carsidarids in having a bipartite male proctiger that bears a median posterior lobe in addition to the lateral lobes. Like *Carsidara* the $M+Cu$ stem is short but this is probably a primitive feature; the pterostigma is absent, resembling some species of *Allocarsidara* but this is likely to be a parallel development in the two genera; the form of the apical segment of the aedeagus and particularly the endtube of the ductus ejaculatorius is similar to *Paracarsidara* and this is considered as a synapomorphy for the two genera.

Included species

A great deal of confusion exists over the identity and validity of the six species currently recognised in this genus. I have not examined original type-material but have seen a large number of specimens from most of the areas from where these species were described. There is considerable variation in size, body coloration and forewing pattern and vein proportions (Figs 36–39) between, but not within, samples, although this variation does not correlate well with hostplant data or geographical distribution. Male and female genitalia and larval morphology are, however, remarkably consistent throughout the geographical and hostplant ranges of the material.

The most commonly encountered species is *M. hibisci* and its hostplant, *Hibiscus tiliaceus*, is common in strandline and coastal vegetation throughout the Pacific and Indian Ocean regions from Polynesia to the East and South African coast. *M. camphorae* and *M. lineaticollis*, both originally described from Taiwan, have been subsequently recorded on *Hibiscus tiliaceus* and other malvaceous hosts such as *Urena lobata* and *Abutilon indicum*, in South East Asia. *M. lutheri*, described from Sri Lanka, is recorded from *Hibiscus tiliaceus* and *Urena lobata* in India, Sri Lanka, Réunion and Madagascar. *M. africana* was described from Natal without host data but there are *Mesohomotoma* samples in BMNH collected from *Hibiscus* in eastern Tanzania, Kenya, Uganda and Zaïre; *M. tessmanni* is widespread in Central and West Africa on *Cola*, *Theobroma* (cocoa) and other sterculiaceus hosts.

I suspect that *camphorae*, *lineaticollis*, *lutheri* and *africana* are synonyms of *hibisci*. Furthermore, there appear no consistent morphological characters, either in the adult or larva, that will separate *tessmanni*

from *hibisci* but the sterculiaceous hostplant preferences of the West and Central African populations suggest some genetic isolation from the Malvaceae-feeding populations. *Hibiscus tiliaceus* does occur around the coastal areas of West Africa but it is not known if these bushes support populations of *Mesohomotoma*. Further collecting here would be useful. Experimental work involving hostplant transfers and crossbreeding techniques is required to clarify the problem.

***Mesohomotoma hibisci* (Froggatt)**

(Figs 36, 37, 77, 78, 89, 94)

Tyora hibisci Froggatt, 1901: 287. Syntypes ♂, ♀, AUSTRALIA: Queensland, on *Hibiscus tiliaceus* (ANIC) [not examined].

Udamostigma hibisci (Froggatt) Enderlein, 1910: 138; Aulmann, 1913: 81.

Mesohomotoma hibisci (Froggatt) Crawford, 1920: 356; 1925a: 34; 1927: 30; Klyver, 1933: 25; Caldwell, 1942: 21; Tuthill, 1943: 71; 1951: 273; 1964: 355; Tuthill & Taylor, 1955: 250; Hodkinson, 1983: 353; 1986: 317; Morgan, 1984: 29.

HOSTPLANTS. *Hibiscus tiliaceus*, *H. rosasinensis*, *H. boryanus* (Malvaceae).

RECORDED DISTRIBUTION. Polynesia (Society, Austral and Rapa Is), Melanesia (Fiji and Solomon Is, New Caledonia), Micronesia (Marianas and Caroline Is), Australia (Queensland).

MATERIAL EXAMINED

Numerous adults and larvae from: **Polynesia** (Cook, Society, Tonga, Samoa and Ellice Is), **Melanesia** (Fiji, Loyalty, New Caledonia, Solomons, Bismark Is and Papua New Guinea), **Micronesia** (Caroline, Marianas and Gilbert Is), **Australia** (N.S.W.), **Indonesia** (Sulawesi), **Philippines**, **Hong Kong**, **India**, **Chagos Arch.**, **Seychelles**, **Réunion**, **Mauritius**, **Madagascar**, **Zaire**, **Uganda**, **Kenya**, **Tanzania**, **Zimbabwe**, **South Africa** (Natal).

***Mesohomotoma africana* Pettey**

Mesohomotoma africana Pettey, 1924: 29; 1925: 138; Capener, 1970: 199. Syntypes ♂, ♀, SOUTH AFRICA (Natal) (NCI; BMNH) [1 ♀ examined].

HOSTPLANT. *Hibiscus* sp. (Malvaceae).

RECORDED DISTRIBUTION. South Africa (Natal).

***Mesohomotoma camphorae* Kuwayama**

Mesohomotoma camphorae Kuwayama, 1908: 181; Aulmann, 1913: 36; Crawford, 1925a: 33; 1927: 31; 1928: 34; Kuwayama, 1931: 123; Takahashi, 1936: 292; Sasaki, 1954: 32; Miyatake, 1964: 123; 1965: 174; 1971: 58; Hodkinson, 1983: 352; 1986: 317; Yang, 1984: 178. Syntypes ♂, ♀, JAPAN (Osagawara Is) and TAIWAN, on 'Kampferbaume' [not examined].

HOSTPLANTS. *Hibiscus tiliaceus*, *H. mutabilis*, *Abutilon indicum*, *Thespesia populnea*, *Urena lobata* (Malvaceae); *Cinnamomum camphora* (Lauraceae) but Sasaki (1954) regards the camphor records as erroneous.

RECORDED DISTRIBUTION. Samoa, Fiji, Philippines, Japan (Osagawara and Ryukyu Is), Taiwan.

***Mesohomotoma lineaticollis* Enderlein**

Mesohomotoma lineaticollis Enderlein, 1914: 232; Crawford, 1925a: 35; Boselli, 1930: 188; Kuwayama, 1931: 123; Braza & Calilung, 1981: 356; Hodkinson, 1983: 353. Holotype ♂, 'FORMOSA' [not examined].

HOSTPLANT. *Urena lobata* (Malvaceae). Also recorded (probably in error) on *Cordia dichotoma* (Boraginaceae).

RECORDED DISTRIBUTION. Taiwan, Philippines.

***Mesohomotoma lutheri* (Enderlein)**

Udamostigma lutheri Enderlein, 1918: 484. Syntypes ♂, ♀, SRI LANKA [not examined].

Tyora indica Crawford, 1919: 159. Syntypes ♂, ♀, AMBOINA and INDIA [not examined]. [Synonymised by Crawford, 1925a: 34.]

Tyor[i]a indica Crawford; Uichanco, 1921: 279. [Misspelling.]

Mesohomotoma lutheri (Enderlein) Crawford, 1925a: 34; 1927: 31; Mathur, 1975: 146; Hodkinson, 1983: 353; 1986: 317.

Mesohom[a]toma lutheri (Enderlein); Orian, 1972: 2. [Misspelling.]

HOSTPLANTS. *Hibiscus* sp., *Urena lobata* (Malvaceae).

RECORDED DISTRIBUTION. Amboina, Philippines, India, Ceylon, Réunion, Madagascar.

Mesohomotoma tessmanni (Aulmann)

(Figs 16, 17, 38, 39)

Udamostigma tessmanni Aulmann, 1912a: 10; 1912b: 101; 1913: 81. Syntypes ♂, 'SPANISH GUINEA' [not examined].

Mesohomotoma (Udamostigma) tessmanni (Aulmann) Cotterell, 1927: 109.

Mesohomotoma tessmanni (Aulmann); Alibert, 1951: 44; Eastop, 1961: 167; Forsyth, 1966: 73; Leston & Gibbs, 1968: 73; Roberts, 1969: 76; Leston, 1973: 322.

Tyora tessmanni (Aulmann) Eastop, 1958: 19; Kaufmann, 1973: 285.

Tyora (Mesohomotoma) tessmanni (Aulmann); Wood, 1980: 174.

HOSTPLANTS. *Cola* spp., *Theobroma cacao*, *Sterculia tragacantha* (see Forsyth, 1966), *Heritiera* spp. (BMNH) (Sterculiaceae); *Desplatzia lutea* (BMNH) (Tiliaceae); *Chytranthus talbotii* (see Forsyth, 1966) (Sapindaceae); *Cleistopholis* sp. (BMNH) (Annonaceae) (possible host misidentification).

RECORDED DISTRIBUTION. Ghana, Nigeria, Equatorial Guinea.

MATERIAL EXAMINED

Numerous adults and larvae from

Sierra Leone (on *Heritiera*, *Cola*, *Theobroma*), **Ivory Coast** (on *Heritiera*), **Ghana** (on *Theobroma*, *Desplatzia*), **Nigeria** (on *Cola*, *Theobroma*), **San Tomé** (on *Theobroma*), **Cameroon** (on *Cola*, *Theobroma*), **Central African Republic** (on *Cola*), **Gabon** (on *Cleistopholis*), **Uganda** (on *Cola*), **Zaire** and **Angola**.

COMMENTS. Cotterell (1927) records this species as a minor pest of cocoa (*Theobroma cacao*) in West Africa, damaging young shoots and shortening internodes, which causes 'bunching'. Wood (1980) summarises that, under conditions of drought and high insolation, heavy infestations cause desiccation and death of terminal buds. However, Kaufmann (1973) reports that when the insects infest the flower buds there is little effect on pod production and the insects may be involved in flower pollination.

Phylogeny, biogeography and hostplants

(Summary Fig. 1)

The Carsidaridae and Homotomidae are considered here to be sister-groups, the pair being characterised as follows: antennal sockets enlarged and giving the head a cleft appearance in dorsal view; paired metapostnotal epiphyses present; ventral sense organs of hind femora situated basally and not arranged linearly. Hostplants of both families are in the Malviflorae (sensu Thorne, 1983). Homotomids have a characteristic bipartite male proctiger and many have a thickened and densely hirsute antennal flagellum, although the *Macrohomotoma*-group of genera have a simple filiform flagellum. All homotomids develop on species of *Ficus* (Urticales) and are distributed mainly in the Old World tropics, but one small genus occurs in Central and northern South America. Two species occur in the Mediterranean Basin on *Ficus carica*, and a third species extends into eastern South Africa on *Ficus petersii*. Carsidarids are diagnosed by the character-suite given on p. 89 and are restricted to hostplants in the Malvales; the group is almost entirely pantropical.

Within the Carsidaridae the Central American genus *Epicarsa* has a distinctive forewing and antennal flagellum; the structure of the male proctiger is unique and the genus is considered to be the sister-group of the rest of the family. The single known species is found on *Ceiba* (Bombacaceae). Apart from *Epicarsa* and the Central and South American genus *Paracarsidara* the rest of the family is distributed in the Old World. *Carsidara* is quite distinct, having highly modified female terminalia and male aedeagal apex; it also retains the primitively broad forewing and very short *M+Cu* stem and has species in tropical Africa, Madagascar and South East Asia

on sterculiaceous hosts. Of the narrow-winged genera *Protyora* is unique in retaining the primitive features of a costal break in the forewing and a simple, flask-shaped male proctiger; it is separated from the rest of the group by the derived state of the aedeagal apex. Two species are known, one in Sulawesi Utara and another in Australia on a sterculiaceous host. The remaining genera are difficult to characterise as a whole; they all possess a male proctiger that is enlarged basally and bears small or large lateral lobes but this character is also shared by *Carsidara* and is not likely to be a parallel development in this genus. Within this assemblage *Tyora* and *Tenaphalara* are grouped together, having an additional r_1 - rs crossvein and hind tibial spurs arranged 1+2+2. *Tyora* species have retained many primitive features, including the presence of radular spinules in cell cu_1 and the close proximity of the apex of the calval suture to the apex of Cu_{1b} ; they are restricted to sterculiaceous hosts in South East Asia. *Tenaphalara* has more derived features, its species occur in both Africa and the Oriental Region on hostplants in the Bombacaceae. *Mesohomotoma*, with species in the Afrotropical, Malagasy, Oriental, Australasian and Pacific Regions, has a distinctive bipartite male proctiger that bears a median posterior lobe; it also lacks a pterostigma in the forewing but this feature is shared, probably by convergence, with some species of *Allocarsidara*. The form of the endtube of the ductus ejaculatorius is similar to that of *Paracarsidara* and this is considered as a synapomorphy for the two genera. *Mesohomotoma* species usually develop on malvaceous hosts but one African species is known to live on various Sterculiaceae. Species of the Central and South American genus *Paracarsidara* develop on both Bombacaceae and Malvaceae. Little is known of the hostplants of the South East Asian genus *Allocarsidara* but three species develop on *Durio zibethinus* (Bombacaceae). The sister-group relationship of *Allocarsidara* is not resolved. It has rounded margins of the vertex, as in *Tenaphalara*, and some of the species lack a pterostigma, as in *Mesohomotoma*, but both these characters are likely to be parallel developments.

A list of characters is given below and the matrix, from which the phylogeny (Fig. 1) was generated, is given in Table 2.

Raven & Axelrod (1974), in their review of angiosperm biogeography, state, with reservations, that the primary radiation of both the Malvales and the Moraceae occurred in Africa and South America in the Upper Cretaceous period. In the Malvales, the Sterculiaceae were the first group to reach Eurasia, followed by the Bombacaceae and then the Malvaceae. This is reasonably congruent with the hostplant preferences of the carsidarid genera. Those displaying more primitive features, e.g. *Carsidara*, *Tyora* and *Protyora*, are on Sterculiaceae, while those with more derived features, e.g. *Tenaphalara*, *Allocarsidara*, *Paracarsidara* and *Mesohomotoma*, are on Bombacaceae and Malvaceae. *Mesohomotoma* is anomalous as its species develop on both Malvaceae and Sterculiaceae, but the Sterculiaceae-feeding habit is restricted to one African *Mesohomotoma* species and may well be a secondarily derived condition.

If Fig. 1 is a good reflection of carsidarid phylogeny, the subgroups must have been differentiated before the complete separation of Africa from South America (100 m.y.B.P.) as elements of the assemblage showing the most derived characters, e.g. *Allocarsidara* + *Paracarsidara* + *Mesohomotoma*, are present today in both continents, and this is unlikely to be through subsequent dispersal from West Africa to the Caribbean. However, this is the weakest part of the projected phylogeny as these genera are not diagnosed as a group.

List of characters

Primitive condition is given in parenthesis

1. Integument of head and thorax sparsely short-setose or almost glabrous. (Integument of head and thorax densely long-setose.)
2. Flagellomeres thickened. (Flagellomeres narrow, elongate.)
3. Flagellomeres thickened and densely hirsute. (Flagellomeres narrow, elongate.)
4. Flagellomere 3 with subapical rhinarium. (Rhinarium absent from flagellomere 3.)
5. Forewing angular apically. (Forewing rounded apically.)
6. Forewing narrow. (Forewing broad.)
7. Costal break absent. (Costal break present.)
8. Pterostigma absent. (Pterostigma present.)
9. R_s and M_{1+2} anastomosing. (R_s and M_{1+1} parallel, not in contact.)

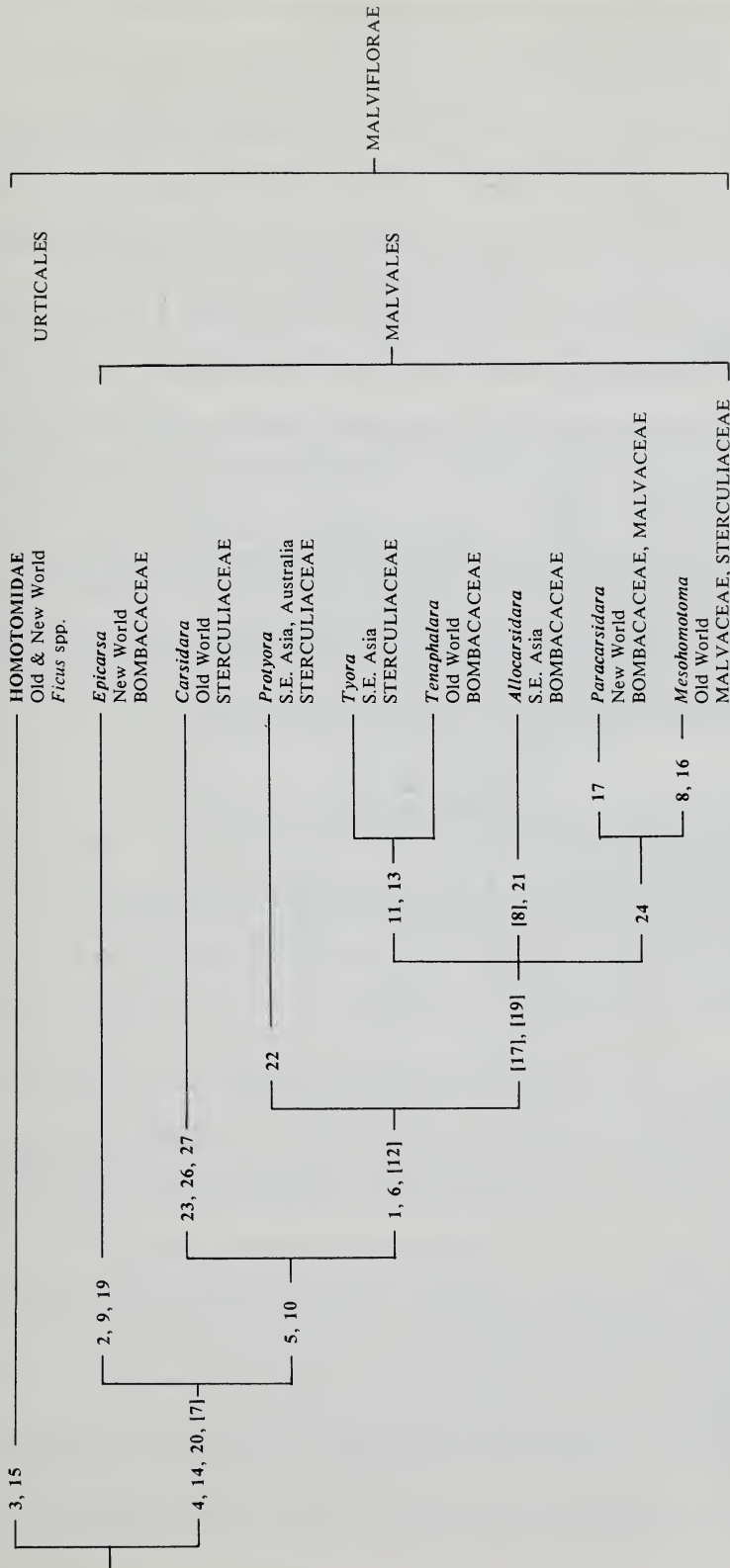


Fig. 1 Summary of phylogeny, distribution and hostplant groups of the *Carsidaridae*. [] denotes character not shared by all members of group. For characters relating to numbers see 'List of characters' in text (p. 109).

10. Non-tracheate *rs-m* crossvein present. (*rs-m* crossvein absent.)
11. Non-tracheate *r₁-rs* crossvein present. (*r₁-rs* crossvein absent.)
12. *M+Cu* stem long. (*M+Cu* stem short.)
13. Apical spurs of hind tibia arranged 1+2+2. (Hind tibial spurs arranged 1+2(or 3)+1.)
14. Metabasitarsus with a single apical spur. (Metabasitarsus with two apical spurs.)
15. Male proctiger bipartite, apical section consisting of a simple anal tube. (Male proctiger unipartite, tubular.)
16. Male proctiger bipartite, apical section having a median posterior lobe in addition to anal tube. (Male proctiger unipartite, tubular.)
17. Male proctiger with enlarged basal portion subdivided posteroapically into small lateral lobes. (Male proctiger tubular.)
18. Male proctiger with well-developed, simple lateral lobes. (Male proctiger tubular.)
19. Lateral lobes of male proctiger each with a secondary inward-pointing lobe. (Secondary, inward-pointing lobes absent.)
20. Male subgenital plate with supplementary lobes. (Male subgenital plate without supplementary lobes.)
21. Inner lateral surfaces of male subgenital plate with patches of spinules. (These spinules not differentiated.)
22. Apex of aedeagus enlarged, endtube of ductus ejaculatorius simple. (Apex of aedeagus narrow, endtube of ductus ejaculatorius simple.)
23. Apex of aedeagus enlarged, complex, endtube of ductus ejaculatorius laterally compressed and heavily chitinised. (Apex of aedeagus narrow, endtube of ductus ejaculatorius simple.)
24. Ductus ejaculatorius with a complex endtube bearing ridges and hooks. (Endtube of ductus ejaculatorius without ridges or hooks.)
25. Female proctiger with a posterodorsal lobe. (Female proctiger without a posterodorsal lobe.)
26. Lateral margins of female proctiger densely long-setose. (Lateral margins of female proctiger sparsely short-setose.)
27. Lateral palps of ovipositor heavily ridged. (Ovipositor palps not ridged.)

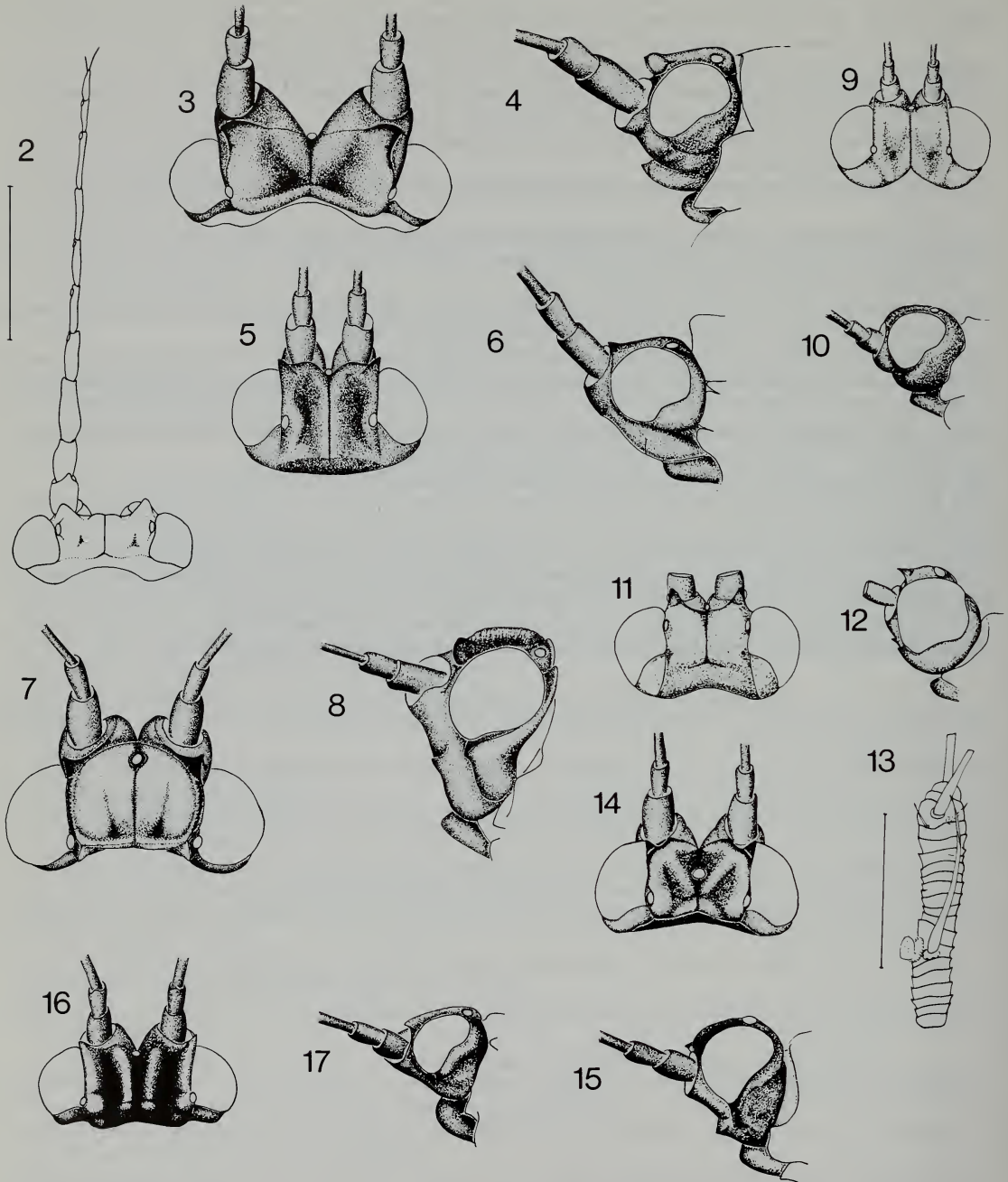
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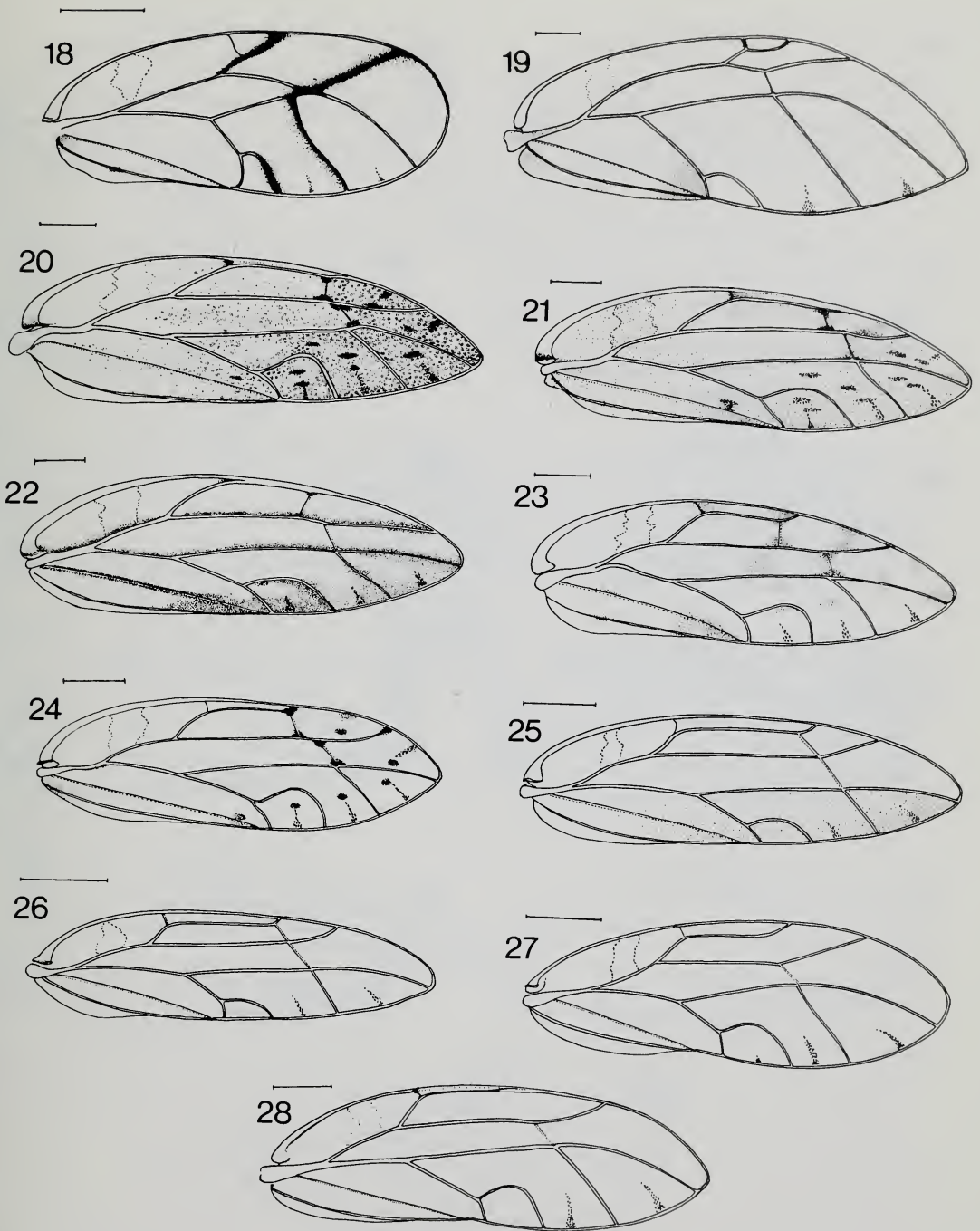
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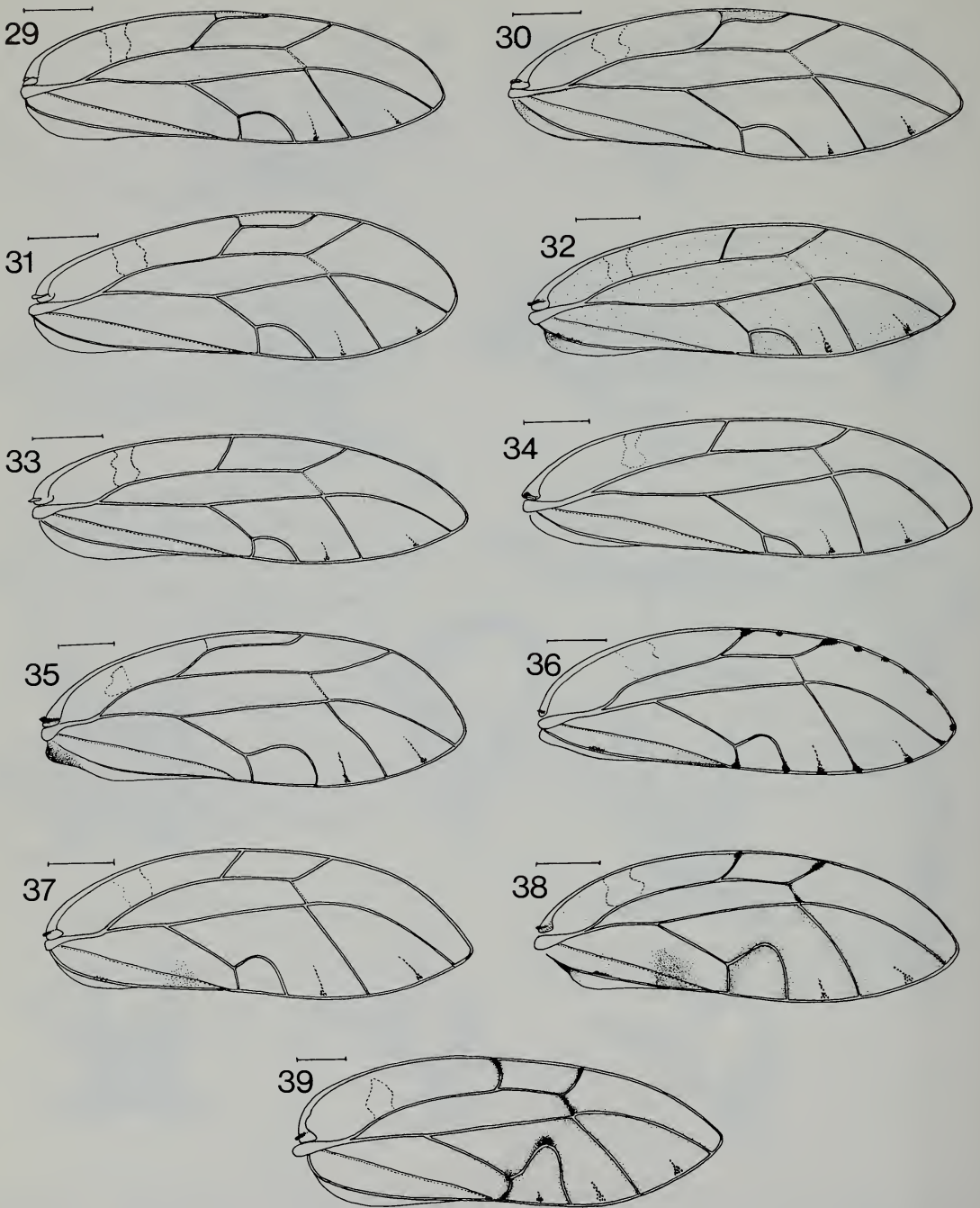
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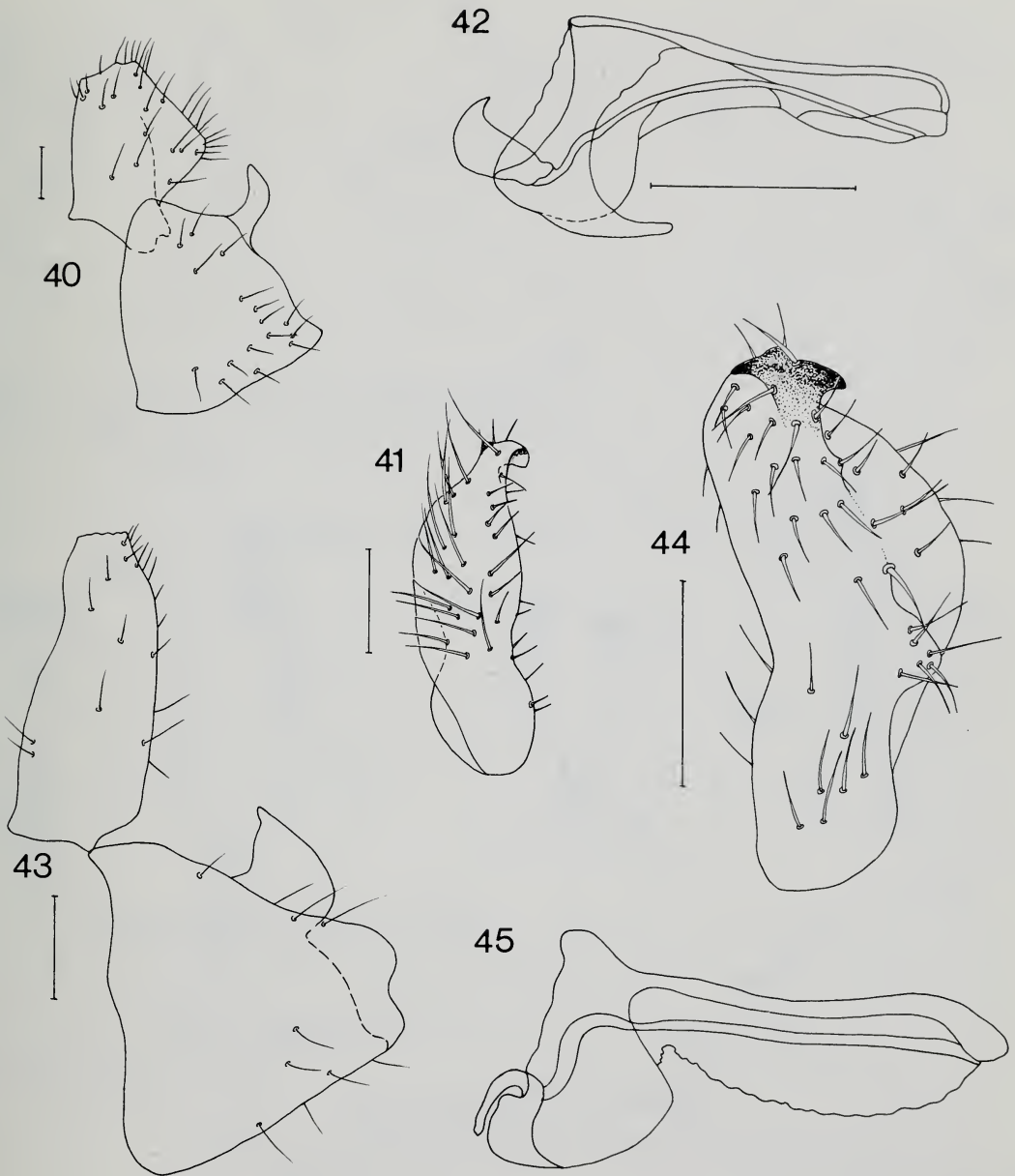
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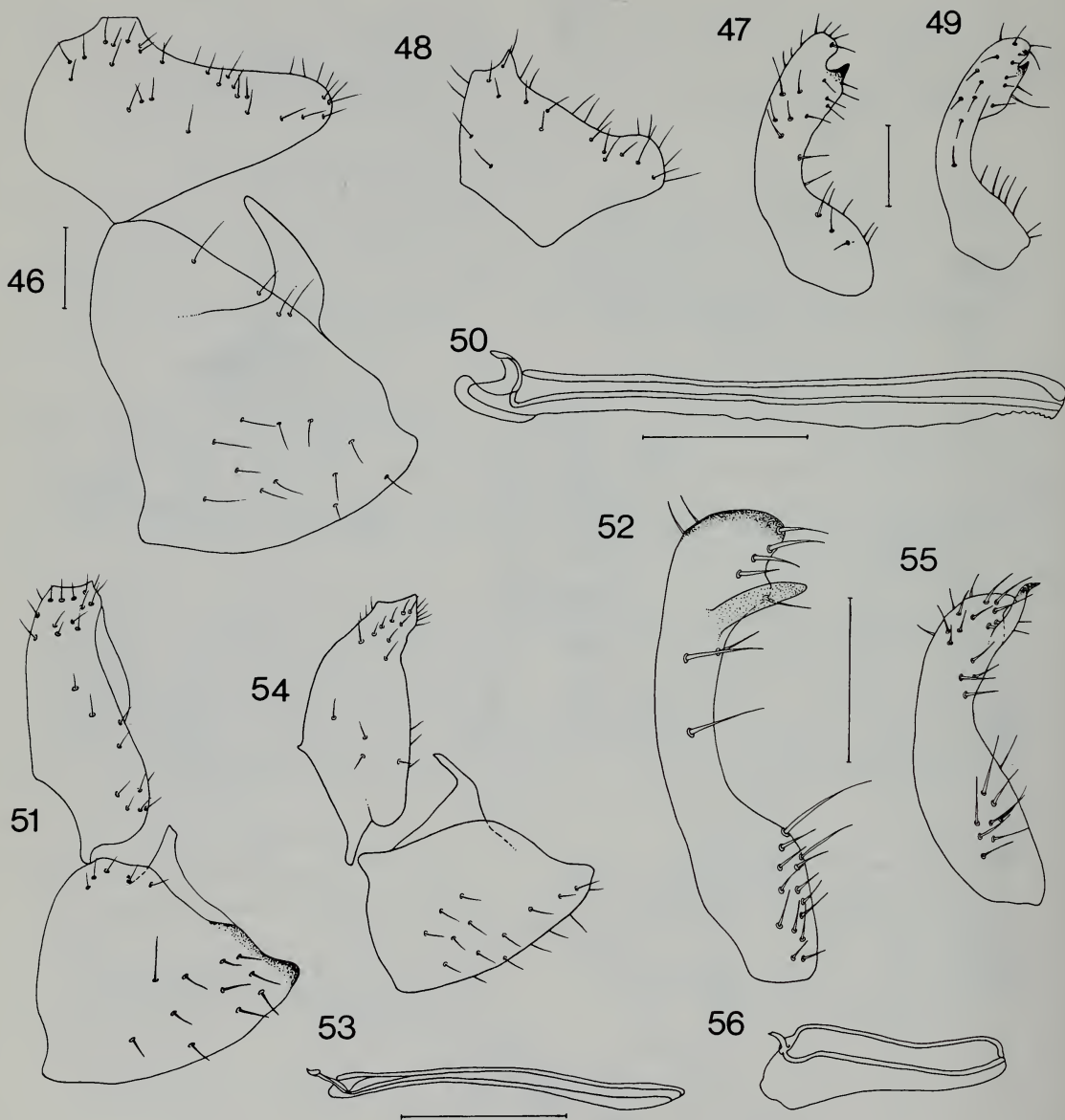
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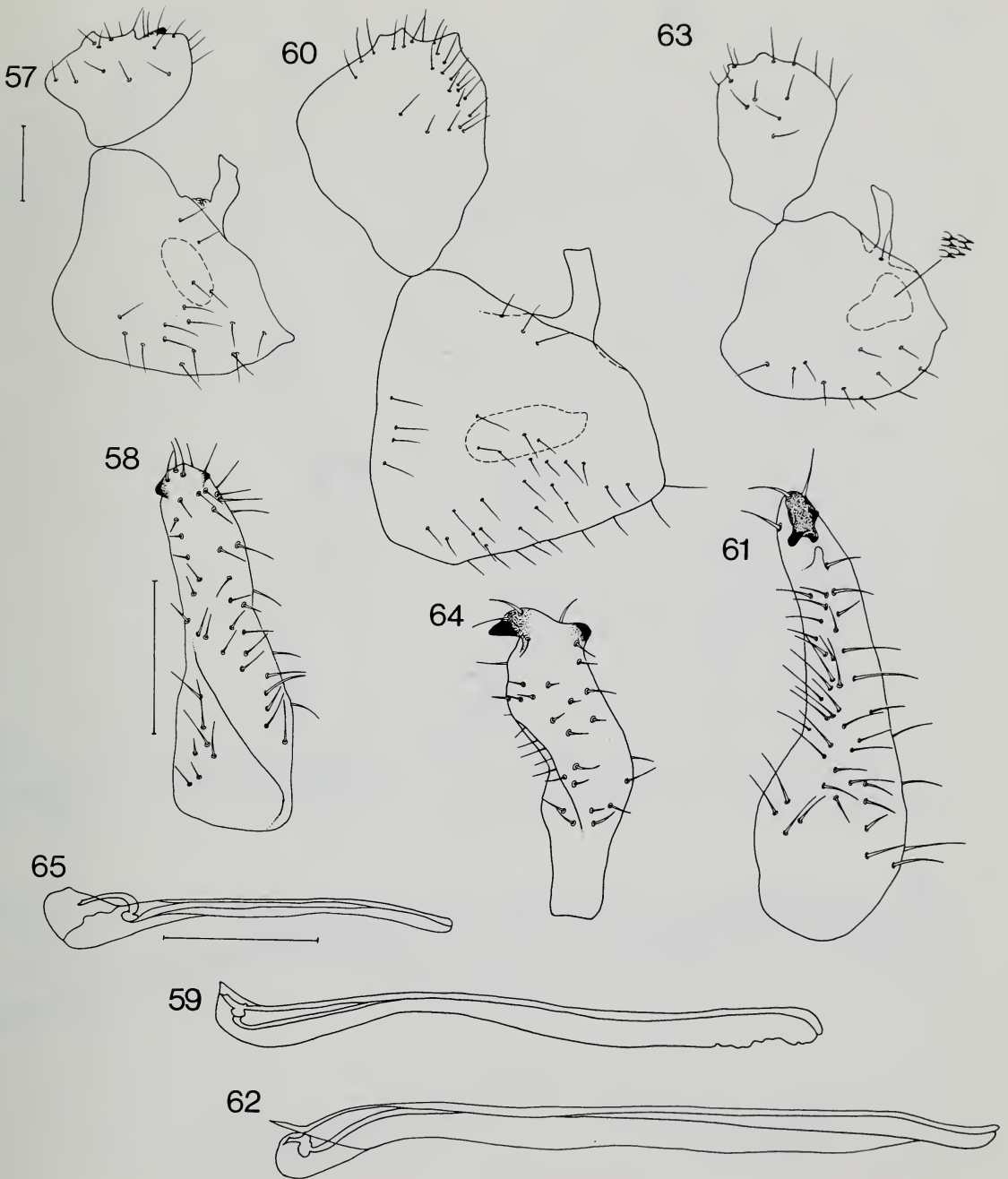
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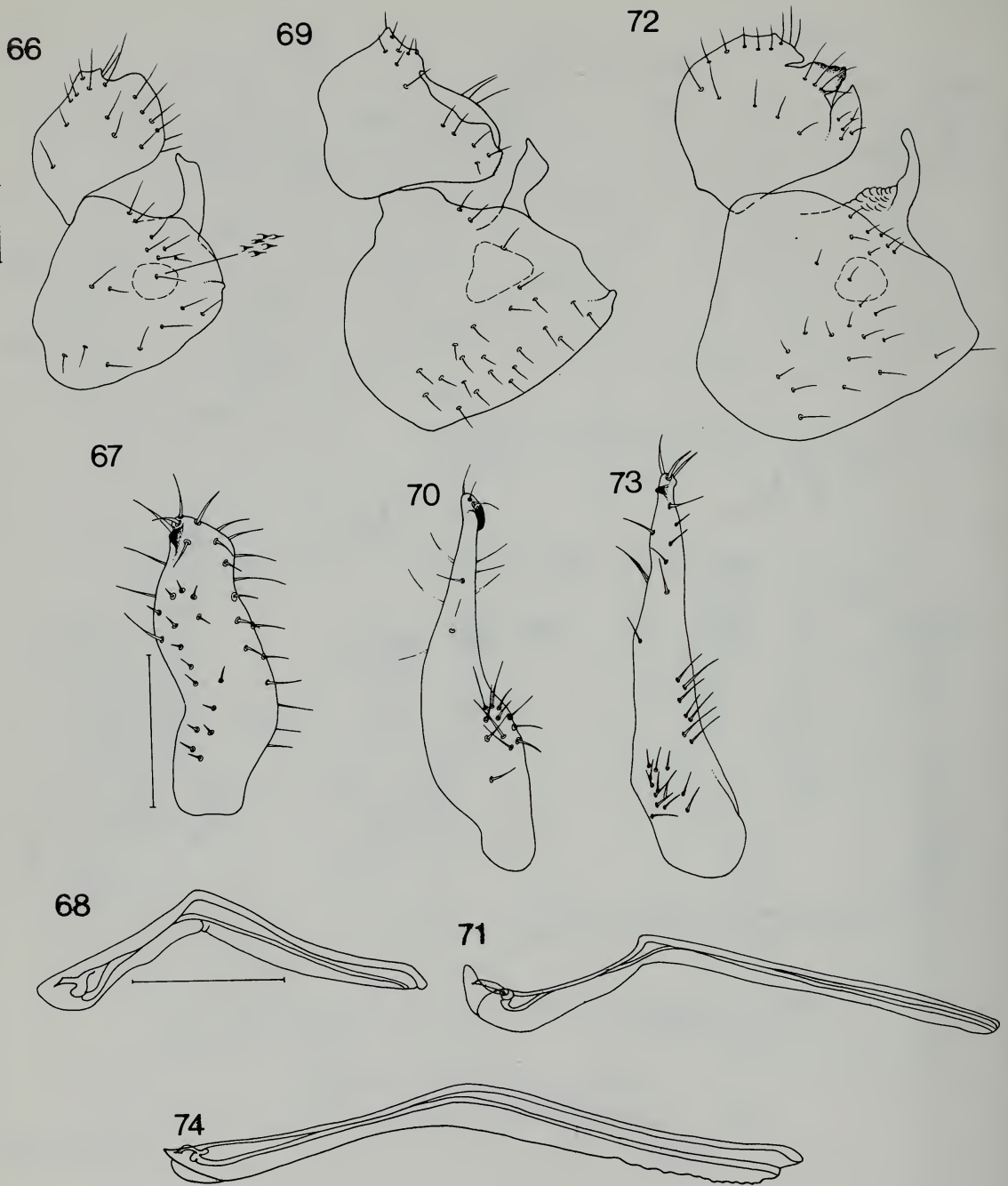
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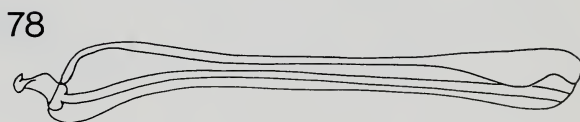
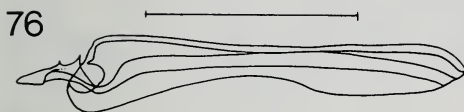
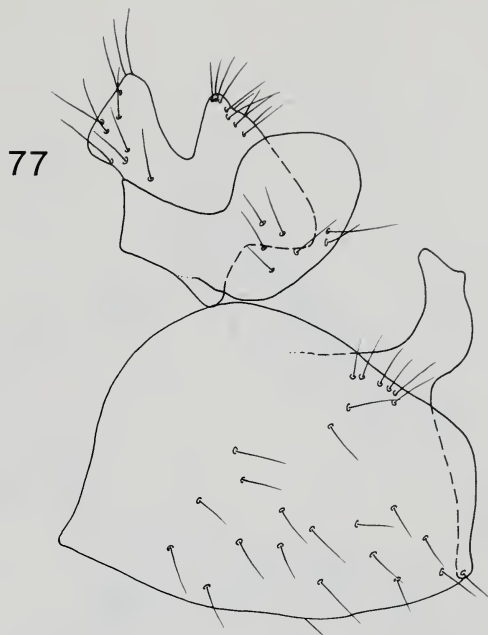
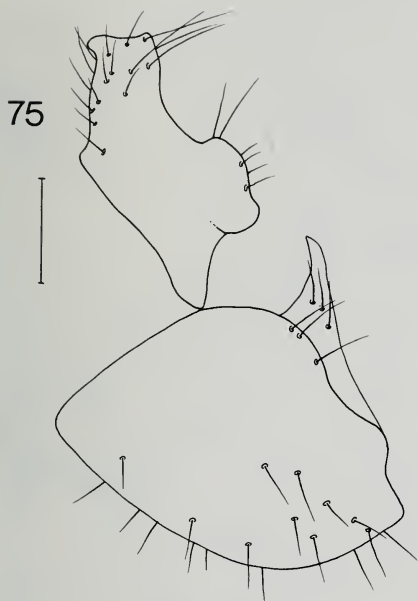
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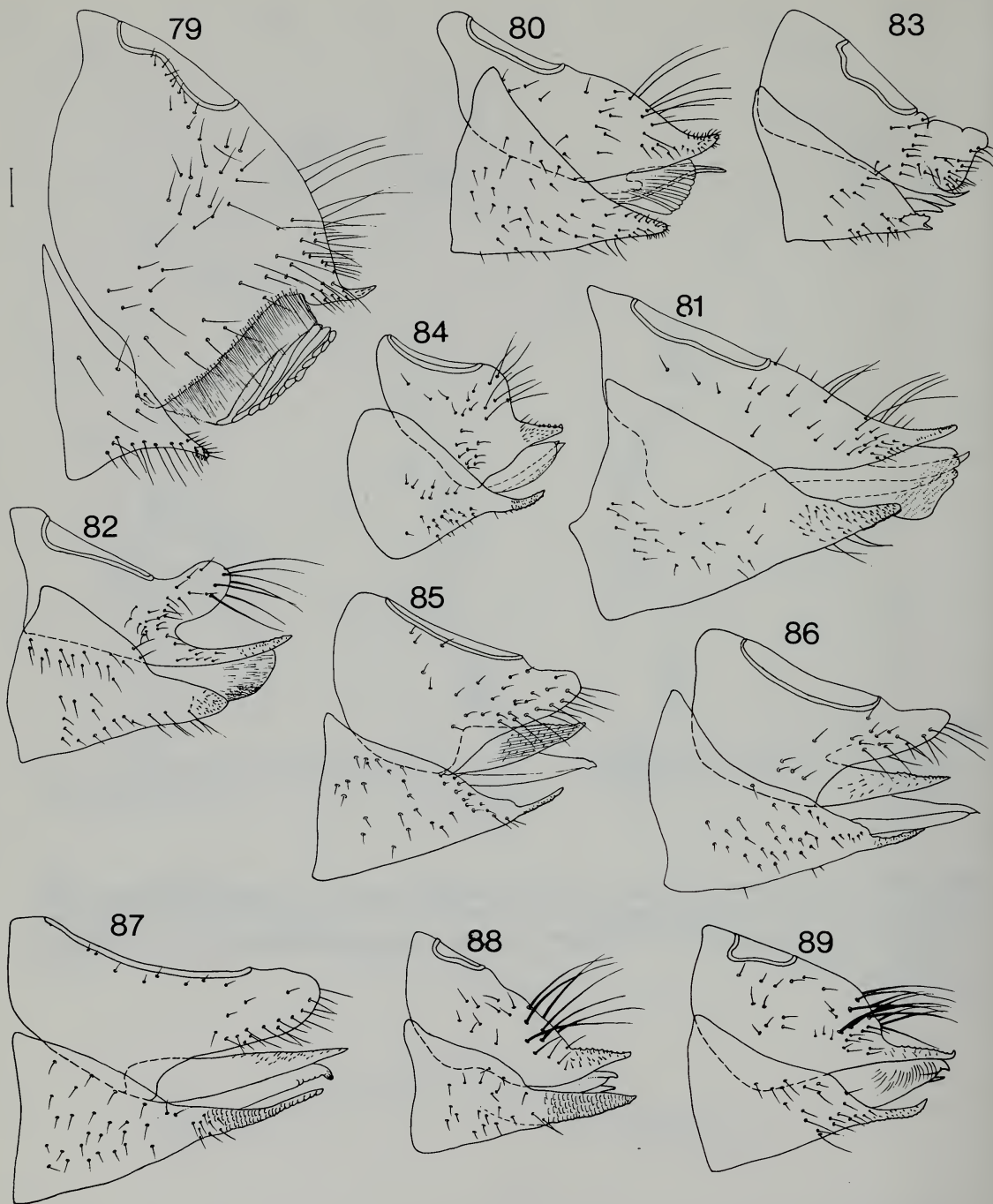
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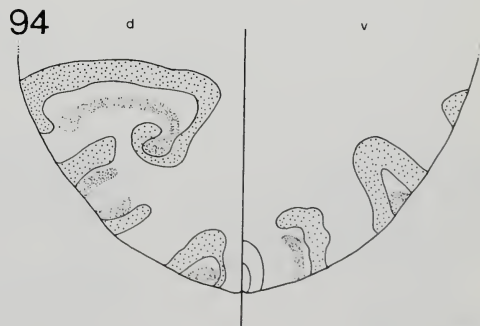
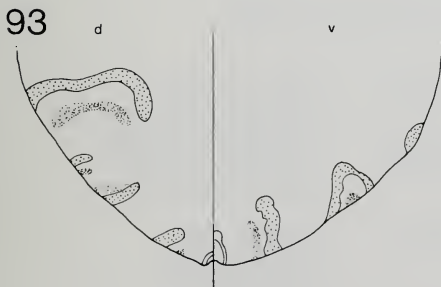
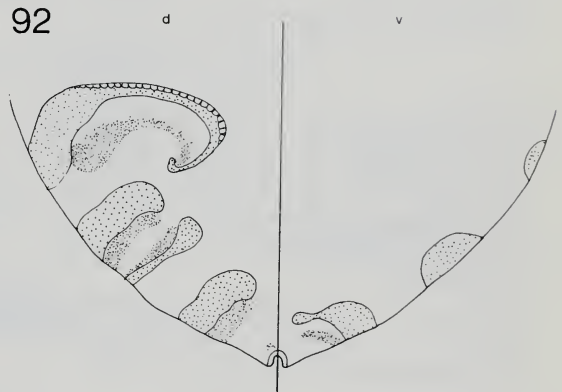
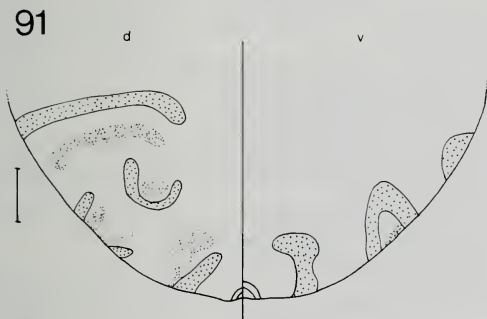
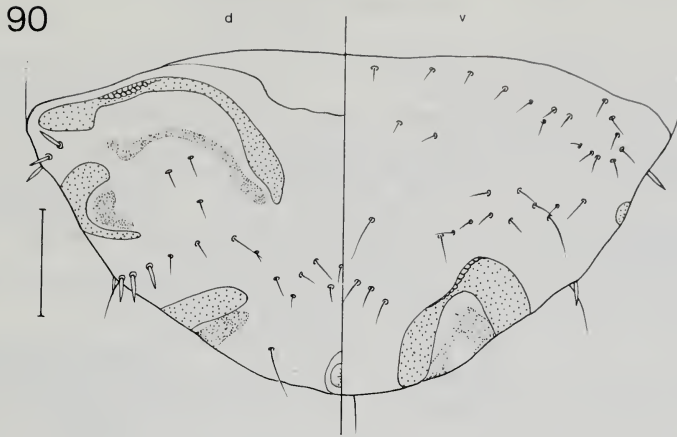
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